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# Factors associated with Atlantic white -cedar seedling recruitment on microtopographic and landscape scales, Brown Mill Pond, Rye, New Hampshire

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# FACTORS ASSOCIATED WITH ATLANTIC WHITE-CEDAR SEEDLING RECRUITMENT ON MICROTOPOGRAPHIC AND LANDSCAPE SCALES, BROWN MILL POND, RYE, NEW HAMPSHIRE

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By

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The decline of Atlantic white-cedar (*Chamaecyparis thyoides*) throughout its range has motivated researchers to investigate cedar seedling recruitment. In this study, conducted at Brown Mill Pond in Rye, New Hampshire, the distribution pattern of cedar seedlings was studied in order to identify which, if any, biological or physical factors observed at a microtopographic scale were associated with seedling presence. On a landscape scale, five previously identified cedar communities were measured for differences in water table level and soil moisture in order to determine associations between stand dynamics and hydrology.

A field survey showed that cedar seedlings were 1) absent from hummocks with tussock sedge substrate and present on hummocks with moss or litter substrate, 2) most frequent 10-25 cm above the July water table, at "intermediate" elevations, and were less common between 25-60 cm on these hummocks.

Several multi-factor field experiments tested whether factors identified in the survey, specifically substrate type and elevation relative to the water table, influenced cedar seedling emergence, growth, or survival. In one set of experiments, seeds and seedlings were transplanted to hummocks having different substrates. In contrast to results of the survey, these experiments indicated substrate type did not influence seedling emergence, growth, or survival. The lack of cedar seedlings on tussock sedge hummocks may be explained by hummock area rather than substrate quality, as tussock sedge hummocks were generally smaller than the moss-litter hummocks. In another set of experiments, seeds and seedlings were transplanted to different hummock elevations where some received supplemental water. The experiments showed that elevation relative to the water table influenced cedar seedling emergence and performance, and that moisture was a primary limiting factor in natural regeneration at this site.

Differences in water table level and soil moisture were associated with differences in species composition and stand structure among the five cedar communities. In the wettest community continuous establishment of cedar was evident, while in the driest community red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) dominated the understory and were expected to replace cedar over successional time.

## INTRODUCTION

Atlantic white-cedar is an uncommon, obligate wetland tree species with limited abundance and distribution throughout its range along the eastern coast of the United States (Laderman 1987, Sperduto and Ritter 1994, Kuser et al. 1997, Zampella and Lathrop 1997, Phillips et al. 1998, Eckert 1998). Cedar populations have decreased in number and size since the time of European settlement (Baldwin 1961, Baldwin 1965, Laderman et al. 1987, Motzkin 1990, Sperduto and Ritter 1994). Decline in the number and size of Atlantic white-cedar populations has generated concern for cedar conservation. In remaining stands the loss of cedar due to succession or inadequate recruitment beneath its own canopy is an important management concern (Motzkin 1990, Kuser and Zimmermann 1995, Allison and Ehrenfeld 1999, Mylecraine and Zimmermann 2000). Recently, there has been much interest in cedar's recruitment requirements and the techniques for regenerating and restoring cedar wetlands (Ehrenfeld 1995b, Kuser and Zimmermann 1995, Mylecraine and Zimmerman 2000).

There are conflicting reports concerning the shade tolerance of Atlantic white-cedar and the role of light in controlling regeneration (Korstian and Brush 1931, Little 1950, Hickman and Neuhauser 1977, Motzkin 1990, Stoltzfus and Good 1998). Other potential limiting factors including microtopography, soil moisture, and substrate may better explain the lack of successful cedar recruitment in some wetlands (Ehrenfeld 1995b, Allison and Ehrenfeld 1999). According to a recent study, moisture is the primary limiting factor in cedar natural regeneration (Kuser and Zimmermann 1995). Both excessive and insufficient moisture may prevent germination and seedling growth

(Ehrenfeld 1995b). Studies identifying microsite factors that explain cedar establishment are limited to New Jersey (Little 1950, Ehrenfeld 1995b, Zimmermann 1997, Allison and Ehrenfeld 1999, Haas and Kuser 1999) and have not as yet been conducted in the northern portion of cedar's range, including New Hampshire. Furthermore, none of the previous studies included field experiments that rigorously tested microsite effects on cedar seedling growth and survival.

While soil moisture may determine cedar seedling distribution patterns at a microtopographic scale, water table depths and seasonal fluctuations likely determine the species composition and structure of stands at the landscape scale (Korstian and Brush 1931, Laderman 1989, Ehrenfeld and Schneider 1990, Ehrenfeld 1995b). As an obligate wetland species (Phillips et al. 1998) cedar is adapted to particular water level fluctuations (Kuser and Zimmermann 1995, Mylecraine and Zimmermann 2000). Although previous studies have suggested that hydrological factors, such as water table depth and flood duration, are important to cedar's long-term persistence, few studies thus far have sufficiently quantified water table depths or soil moisture in relation to cedar distribution and stand structure (Golet and Lowry 1987).

Unlike the majority of the even-aged, monospecific, Atlantic white-cedar wetlands in the northern portion of cedar's range (Sperduto and Ritter 1994, Stockwell 1999), stands at Brown Mill Pond in Rye, New Hampshire, showed variation in structure and one stand demonstrated substantial natural cedar regeneration. In previous fieldwork (Gengarelly 1999), five communities were identified at Brown Mill Pond and successional dynamics were determined based on an analysis of the size and age structure of these cedar stands. In the *mixed conifer community*, cedar was being replaced by eastern hemlock and red spruce, a successional pattern not previously reported for cedar. Moreover, successful cedar establishment was found only in an uneven-aged stand, the *pond edge community*, where the canopy was discontinuous (Gengarelly 1999). Preliminary measurements of water table depth in 1998 indicated the mixed conifer community had the lowest water table while the pond edge community had the highest water table in the site. I hypothesized that hydrology differentiated these communities. Given our current understanding of cedar regeneration and distribution, and given the unique characteristics of Brown Mill Pond, my objectives were:

1. To determine the microsite factors that influence cedar recruitment at Brown Mill Pond via a field survey (Chapter I) and field experiments that subsequently test the most significant factors identified by the survey (Chapter II).
2. To determine to what extent the five Brown Mill Pond communities differ in water table depth and soil moisture content when measured over several growing seasons (Chapter III).

# CHAPTER I

## MICROSITE HETEROGENEITY AND ATLANTIC WHITE-CEDAR SEEDLING DISTRIBUTION


### Abstract

The decline of Atlantic white-cedar throughout its range has motivated researchers to investigate cedar seedling recruitment. In this study, conducted at Brown Mill Pond in Rye, New Hampshire, the distribution pattern of cedar seedlings was studied in order to identify which, if any, biological or physical factors were associated with seedling presence. Seedlings occurred on hummocks that rose above the water-filled hollows. However, some hummocks lacked seedlings and most others were only partly covered by seedlings. Thus, three types of microsites were identified: seedling present, seedling absent, seedling missing. Seedling present plots were characterized by at least three cedar seedlings present on a hummock in a 20 x 20 cm area (n = 57). Seedling absent plots (n= 57) were situated on hummocks that did not contain cedar seedlings. Seedling missing plots (n =57) lacked seedlings but occurred on hummocks that included other microsites with seedlings. Environmental variables, i.e., elevation relative to the water table, percent canopy cover, substrate type, shrub density, and distance to nearest prospective parent tree, were measured in each plot. To determine if seedling presence and absence could be predicted from the measured environmental variables, a standard discriminant function analysis was performed.

Substrate type and elevation relative to the water table best explained

the seedling distribution pattern at Brown Mill Pond. Seedlings were absent from hummocks with tussock sedge substrate and present on hummocks with some alternative substrate (i.e., moss or litter). When present on a hummock, seedlings occurred at low to intermediate elevations (10-25 cm) above the water table and were missing from the highest elevations (> 30 cm). This survey identified specific microhabitats correlated with cedar recruitment in a New Hampshire wetland.

## Introduction

### Atlantic White-Cedar: A Tree in Need of Conservation

Atlantic white-cedar (*Chamaecyparis thyoides* (L.) BSP) is a rare, freshwater wetland tree species restricted to the eastern coast of United States (Sperduto and Ritter 1994, Sheffield et al. 1998). Throughout its geographic range, including New Hampshire, *C. thyoides* populations have decreased in number and size since colonial times, which has generated much concern for cedar conservation (Laderman et al. 1987, Motzkin 1990, Sperduto and Ritter 1994, Eckert 1998). Losses of cedar have been partially attributed to successional change in which older cedar stands are replaced by more shade-tolerant tree species such as red maple, *Acer rubrum* L. (Buell and Cain 1943, Little 1950, Motzkin 1990). The threat of succession is evidenced in the minimal successful cedar recruitment beneath its own closed canopy (Motzkin 1990). The decline of Atlantic white-cedar has recently drawn attention to the recruitment requirements of this species (Kuser and Zimmermann 1995, Allison and Ehrenfeld 1999, Haas and Kuser 1999).

### Recruitment Requirements & Distribution of Woody Seedlings

In general, successful tree seedling recruitment is based on the suitability of a site for seed germination and seedling establishment (Grubb 1977, Harper 1977, Huenneke and Sharitz 1986 and 1990, Titus 1990, Schupp 1995). Each species is expected to have a unique set of conditions that form its 'safe site': a favorable location for establishment, survival, and growth of seedlings (Harper 1977, Grubb 1977). Factors that determine a safe site for a species include microtopography, soil moisture, light availability, competition, soil nutrients, and herbivory (Harper 1977). Variability in these factors influences the differential survival of seedlings and in turn affects the spatial distribution of seedlings (Titus 1990, Schupp 1995). According to Schupp (1995), at the seedling stage of development habitat choice is "imposed" on plants by characteristics of the environment.

In wetland forests, seedling recruitment patterns are associated with environmental heterogeneity on the microhabitat scale and differential survival of seedlings among microsites. (Here, the term "microsite" is defined as a volume of space the size of one or a few seedlings.) In a South Carolina cypress-tupelo swamp, Huenneke and Sharitz (1986) showed that water tupelo (*Nyssa aquatica* L.) seedlings were distributed nonrandomly among available microsites. In this frequently flooded site, water tupelo seedlings preferred microsites that were stable substrates and subjected to minimal erosional scour (Huenneke and Sharitz 1990). Similarly, Titus (1990) examined woody seedling distribution patterns in relation to the heterogeneity of substrates due to microtopography in a Florida wetland. Tree seedlings were found more frequently on elevated soil (i.e., hummocks) than on the swamp bottom, while shrubs generally occurred on elevated woody objects (i.e., logs and stumps).

## Conditions Predictive of Cedar Recruitment

Typically, Atlantic white-cedar swamps are defined by a network of elevated hummocks and frequently water-filled depressions or hollows (Ehrenfeld 1995a, Stoltzfus and Good 1998). Cedar commonly occurs on hummocks and it has been suggested that hummock microtopography, as it affects moisture availability, may be an important factor explaining cedar seedling distribution on hummocks (Ehrenfeld 1995a, Ehrenfeld 1995b). According to Ehrenfeld (1995b), cedar seedlings were most common at intermediate elevations on hummocks avoiding the lowest and highest elevations. Perhaps seedling recruitment is unsuccessful at the top of hummocks and at the lowest elevations in the hollows because of drought and prolonged flooding respectively.

Moisture is considered one of the critical factors for Atlantic white-cedar regeneration (Little 1950, Laderman 1989). Both excessive and insufficient moisture may prevent germination and seedling growth (Mylecraine and Zimmermann 2000). According to Little (1950), moisture conditions were optimal for seedling growth if the water table was within 5" (12.7 cm) of the ground surface. In a more recent greenhouse experiment, cedar seedlings achieved greatest growth in moist drained soil, intermediate growth in saturated soil, and the least growth in inundated soil conditions (Allison and Ehrenfeld 1999).

Furthermore, Atlantic white-cedar recruitment is affected by the understory light regime (Little 1950, Mylecraine and Zimmermann 2000). Little (1950) found that cedar required approximately 30% full sunlight for 32-50% cedar germination. When light intensity was less than 16% full sunlight, germination was reduced to 8%. Furthermore, Little (1950) observed a strong decline in cedar seedling survival when seedlings were located beneath the heavy shade of a closed canopy.

Other studies have indicated that open seed beds free of competing vegetation are necessary for cedar establishment (Korstian and Brush 1931, Buell and Cain 1943). In North Carolina, cedar seedlings were most abundant in sites where no competition with understory vegetation existed (Buell and Cain 1943).

The presence of nearby parent trees may also contribute to cedar seedling recruitment. According to Allison and Ehrenfeld (1999), cedar seedlings were most abundant beneath a cedar canopy, suggesting dispersal was greatest near parent trees.

Allison and Ehrenfeld's (1999) field survey also indicated differences in cedar and red maple recruitment based on microsite variations in substrate. While both cedar and red maple seedlings occurred on *Sphagnum*, cedar was more abundant on cedar-needle litter than was red maple, which was commonly found growing among graminoids (Allison and Ehrenfeld 1999). According to accompanying greenhouse experiments, cedar and red maple growth differed in response to varying soil type (peat vs. *Sphagnum*), with cedar growth better than maple in peat soil. Thus, in the New Jersey Pinelands, cedar growth is more successful in peat soil (Allison and Ehrenfeld 1999).

In general, some microsites are favorable for wetland tree seedling establishment while others are unfavorable. For instance, wetland tree seedlings generally grow more frequently or better on elevated soil (i.e., hummocks) than stumps, logs, or roots (Huenneke and Sharitz 1990, Titus 1990, Allison and Ehrenfeld 1999). Furthermore, in a variety of wetland systems tree seedlings “avoid” standing water, which is often present in swamp bottoms or hollows (L. Gengarelly, personal observation, Allison and Ehrenfeld 1999). However, the types of available microsites are expected to vary among wetlands and to differently affect the recruitment pattern of tree seedlings. Consequently, the microsites that form a particular species' safe site may be location specific. Acknowledging that seedling distributions reflect recruitment requirements and site availability per swamp, it is critical to conduct field surveys that describe seedling distributions and identify those conditions most predictive of seedling survival and growth throughout cedar's geographic range. The distribution of cedar seedlings in relation to microsite variability has yet to be investigated in the northern part of cedar's range, including coastal New Hampshire.

Thus, the objective of this research was to identify which, if any, biological or physical conditions were associated with Atlantic white-cedar presence at Brown Mill Pond in Rye, New Hampshire. More specifically, this study investigated the presence and absence of seedlings among microsites in relation to elevation above the water table, percent canopy cover, hummock substrate type, shrub density, and distance to nearest prospective parent tree.

## Methods

### Study Area

This study was conducted during the summer of 2000 in a cedar wetland at Brown Mill Pond in Rye (Rockingham County), New Hampshire. The Nature Conservancy owns the wetland. The soils have been classified as a Chocorua mucky peat and hummock-hollow microtopography is well-developed (Kelsea and Gove 1994).

Elevation is 30 ft above sea level (9 m; Sperduto and Ritter 1994). Cedar dominates some areas of this 110 acre (45 ha) wetland while in others it mixes with *Acer rubrum* (red maple), *Tsuga canadensis* (eastern hemlock), and *Picea rubens* (red spruce). In previous fieldwork (Gengarelly 1999), the site was divided into five communities or stands based on tree species composition, cedar diameter, and cedar height (Figure 1).

The seedling field survey was conducted in the *pond edge community*, which borders Brown Mill Pond and its tributary, Bailey Brook (Figure 1). This community was selected for the survey as it was characterized by an uneven-aged cedar stand with continuous cedar establishment (Gengarelly 1999). This stand was also distinguished by a discontinuous cedar-red maple canopy and the highest water table in the site (Gengarelly 1999, Chapter III).

Two types of hummocks were identified based on the dominant surface substrates. *Tussock sedge hummocks* were characterized by a tussock sedge (*Carex stricta*) substrate consisting of a network of vertical rhizomes intertwined with fine roots and decomposing organics, such as leaf litter (Lord and Lee 2001). *Moss-litter hummocks*, on the other hand, were characterized by a carpet of mosses, including *Sphagnum* spp., *Dicranum* spp., and other taxa, and areas lacking mosses (i.e., litter-covered substrate). Moss-litter covered hummocks are commonly described in other cedar wetlands, especially in New Jersey, and referred to simply as peat hummocks (Ehrenfeld 1995a). In this study, hummocks were differentiated based on their surface substrate and are referred to accordingly as tussock sedge or moss-litter hummocks.

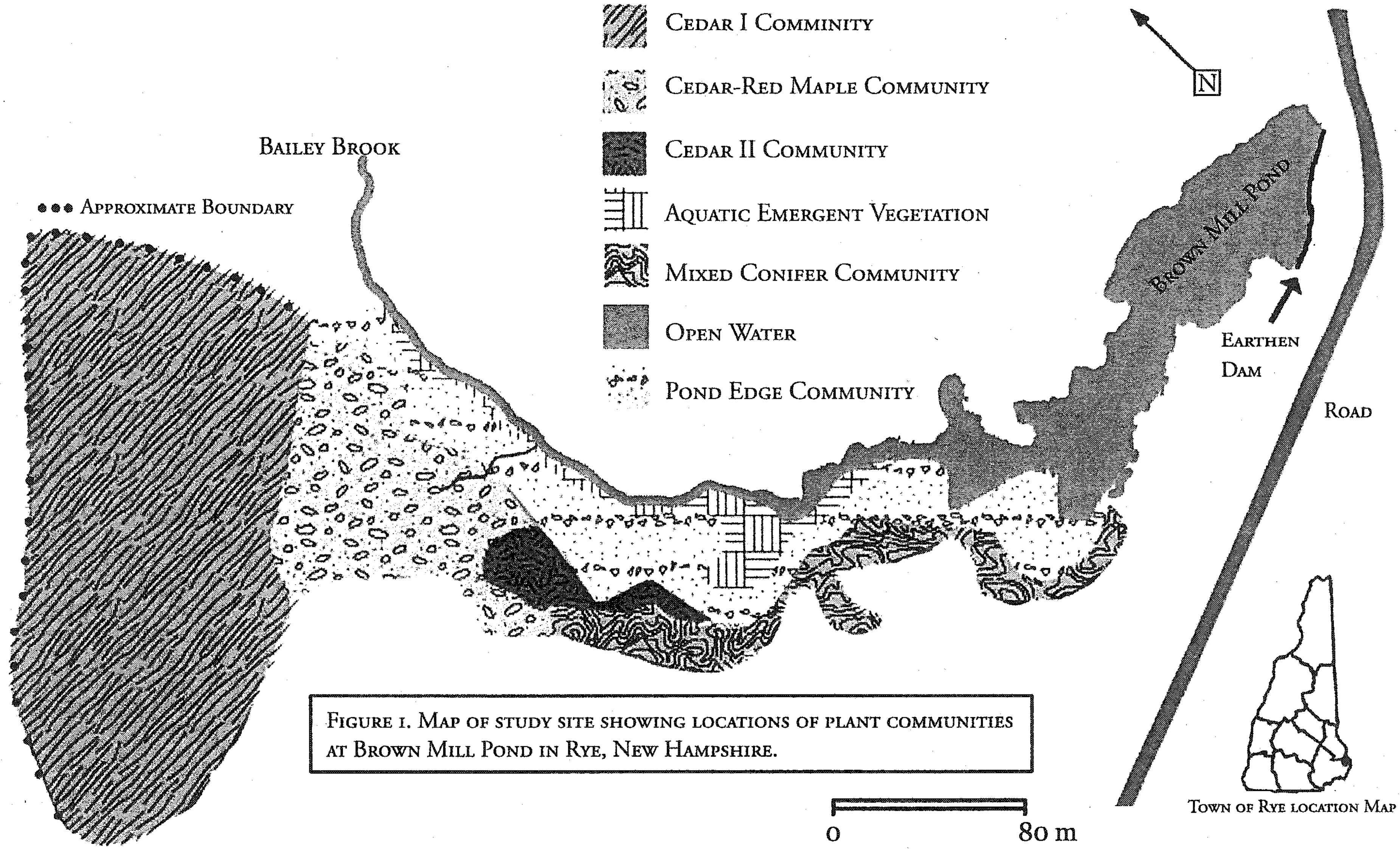



Figure 1. Map of study site showing locations of plant communities at Brown Mill Pond in Rye, New Hampshire.

## Sampling Design

Initial field reconnaissance suggested that some hummocks had seedlings present and that these seedlings occurred in scattered clumps. Other hummocks lacked seedlings altogether. This initial observation indicated that cedar seedling distribution at Brown Mill Pond could be described as "seedling present" microsites, characterized by a cluster of seedlings, "seedling absent" microsites, located on hummocks that did not contain seedlings, and "seedling missing" microsites which lacked seedlings but occurred on hummocks that supported seedlings on other microsites (Figure 2).

The sampling design constructed to capture this striking pattern included thirteen transects (10-15 m in length), randomly located in the pond edge community such that they extended perpendicularly away from the pond and brook. All hummocks greater than 15 cm in elevation relative to the hollow surface and within two meters of either side of the transect were mapped, numbered, characterized for substrate type, surveyed for cedar seedlings, and measured for area. Hummock area was determined by measuring the length and width of a hummock and using the ellipse formula (Area = $\pi$ Length*Width/4). Any cedar displaying some scale-like foliage (suggesting that seedlings were at least in their second growing season) and a height between 5 and 30 cm was considered a seedling. The number of seedlings was recorded for each hummock. Hummock substrate type was also recorded. Newly germinated cedar individuals were excluded, as seeds may germinate in microsites that later prove unsuitable for long-term survival.

Along each transect approximately 15 randomly located 20 x 20 cm plots were

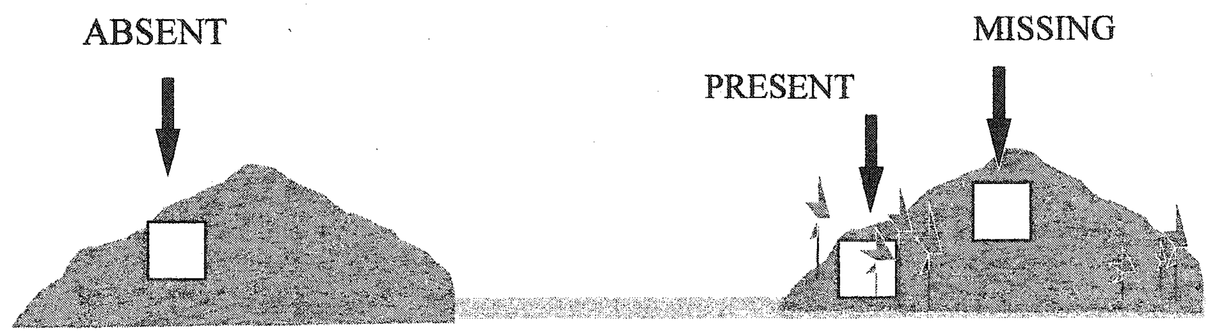



Figure 2. Schematic diagram illustrating the initial observed pattern of Atlantic white-cedar (*Chamaecyparis thyoides*) seedlings on hummocks at Brown Mill Pond, Rye, New Hampshire. Squares indicate the placement of sampling plots used to investigate the three seedling situations at this site.

studied. Plots fell into one of three categories: seedling absent, seedling missing, and seedling present (Figure 2). New random locations were generated until an equal number of plots of each type was sampled. Seedling absent plots were situated on hummocks that did not contain cedar seedlings while seedling missing plots sampled sections of seedling-present-hummocks without seedlings. All seedling missing plots were a minimum of 30 cm from any given cedar seedling. Seedling present plots contained at least three cedar seedlings. In the end, 57 of each type of sampling plot (i.e., absent, missing, or present) were observed.

**Microsite Characteristics**

Within each plot, selected environmental variables were measured. Percent cover of substrate types--tussock sedge, leaf litter, moss--was determined by projecting 100 dots over the 20 x 20 cm plot and recording the substrate intercepted by each dot. Densities of all herbaceous and shrub species were measured. In order to determine elevation, the vertical distance from the center of the plot to the water table was measured using a line level and meter stick. Elevations were adjusted to a single water table height in July (7/3/00). Thus, the July 2000 water table was used as the reference elevation. Percent open canopy was quantified using a digital camera with a fish-eye lens and images were processed with Gap Light Analyzer (Frazer et al. 1999). All photographs were taken at a height of 5 cm. Parent tree proximity was the mean distance between the center of the plot and the two closest reproductive adult cedars.

**Statistical Analysis**

In order to determine if plots with cedar seedlings, without seedlings, and missing seedlings could be predicted from the measured environmental variables, a standard discriminant function analysis was performed (i.e., all predictors entered in one step). The analysis was performed with SPSS 9.0 (Norusis 1999). The seven predictor variables were: elevation relative to the water table, % open canopy, % moss substrate, % leaf litter substrate, % tussock sedge substrate, herbaceous and shrub density, and distance to nearest prospective parent. Three seedling groups were tested, with group membership established prior to the analysis and based on seedling plot type. Group 1 consisted of the seedling present plots (n = 57), group 2 consisted of the seedling missing plots (n = 57), and group 3 consisted of seedling absent plots (n = 57).

A standard multiple regression was performed between cedar seedling number per hummock as the dependent variable and hummock substrate type (tussock sedge vs. moss-litter), hummock area, and the appropriate interaction term (i.e., substrate type x area) as independent variables. In order to improve the normality and linearity of the residuals, square root transformations were used on the seedling number and hummock area measures. This analysis was made using SYSTAT 5.2 for PC (Wilkinson et al. 1992).

## Results

### Discriminant Function Analysis

The three seedling groups--present, absent, missing--differed in their relationship with the environmental variables as described by the discriminant functions. As there were three groups; seedling present, seedling missing, and seedling absent; two discriminant functions were created in this analysis. Together, these discrimant functions

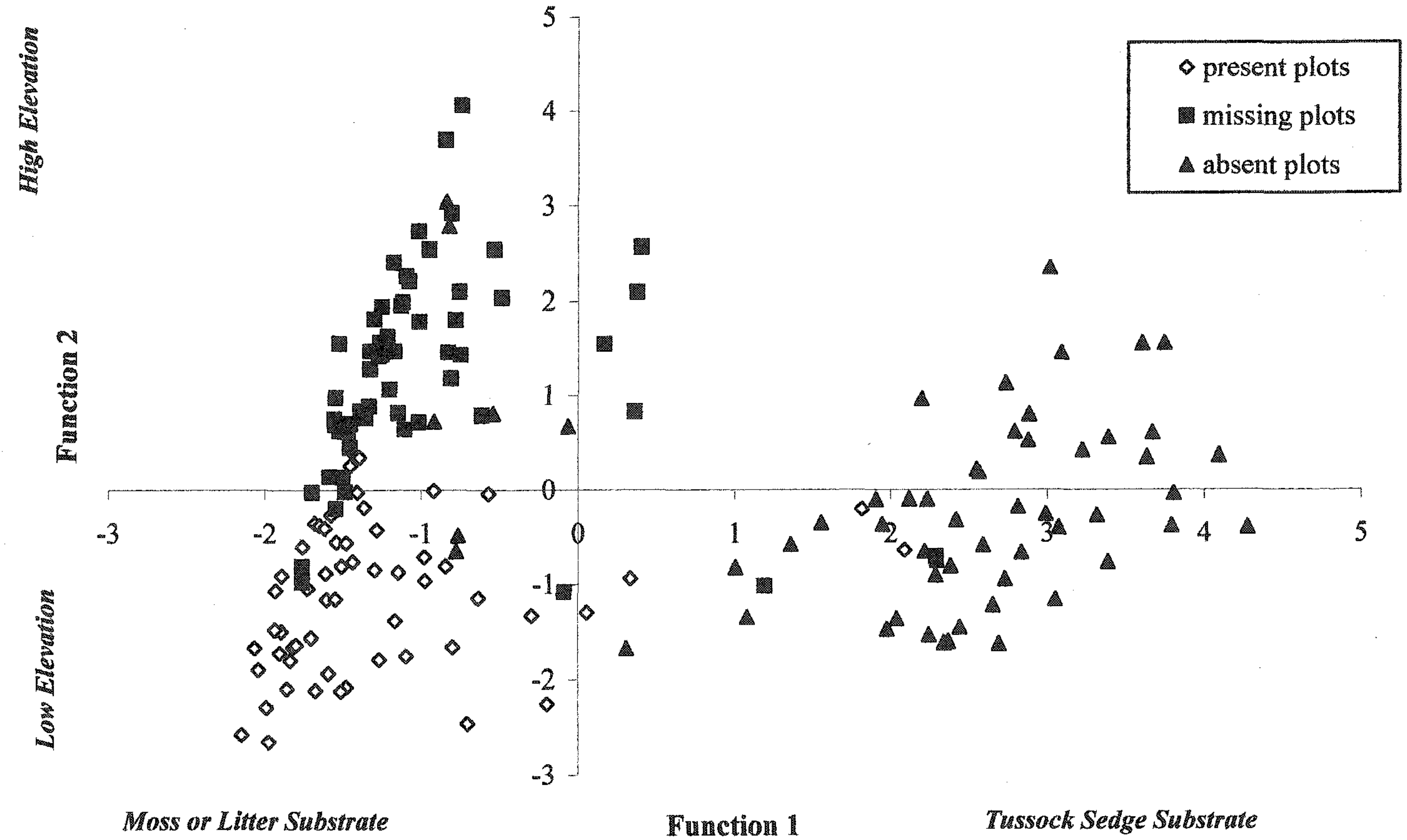



Figure 3. Discriminant function analysis testing the predictability of Atlantic white-cedar seedling groups (seedling present, seedling absent, seedling missing) at Brown Mill Pond, Rye, New Hampshire based on several enviromental variables (July 2000). Discriminant axes scores for all plots in each membership group (n =57) . The x-axis respresents scores on discriminant function one. The y-axis represents scores on discriminant function two. Italicized labels indicate the predictor variable most strongly related to low or high scores on each function.

Table 1. Results of discriminant function analysis that tested the predictability of Atlantic white-cedar seedling groups (seedling present, seedling absent, seedling missing) at Brown Mill Pond, Rye, New Hampshire, based on several environmental predictor variables (July 2000). The standardized canonical discriminant function coefficients for each predictor variable and each discriminant function are presented.

| | Standardized Canonical Discriminant Function Coefficients | |
|---|---|---|
| Predictor Variable | Function 1 | Function 2 |
| Elevation Relative to Water Table (cm) | 0.170 | 0.958 |
| % Open Canopy | 0.016 | -0.099 |
| % Moss Substrate | -0.471 | -0.251 |
| % Litter Substrate | -0.482 | 0.103 |
| % Tussock Substrate | 0.378 | 0.043 |
| Herb and Shrub Density | 0.254 | 0.109 |
| Distance to Nearest Parent Tree (cm) | 0.356 | 0.180 |

successfully and significantly predicted group membership of plots (Wilk's lambda = 0.14; $\chi^2 = 320.81$; df = 14, $p < 0.001$). Specifically, 86% of the variance in the discriminant scores, which are a function of the measured environmental variables, was explained by group membership. Furthermore, each discriminant function alone explained a significant proportion of the variance in the discriminant scores, with the first discriminant function ($r_c = 0.85$, $p < 0.001$) more strongly related to group membership than the second discriminant function ($r_c = 0.70$, $p < 0.001$). Therefore, the three seedling status groups differed in some combination of scores of the environmental parameters as described by the discriminant functions.

Certain environmental variables were most informative about seedling group membership. The first discriminant function (DF1) showed that seedling absent plots (plots on hummocks lacking any cedar seedlings) occurred most often on hummocks with tussock sedge substrate, while the other two kinds of plots occurred most often on hummocks with either moss or litter substrate. This statement is justified because all the substrate predictors (i.e., % moss, % litter, and % tussock) had relatively large ($\geq 0.378$) standardized discriminant coefficients on DF1 (Table 1) with high scores on DF1 associated with both tussock sedge substrate (Table 1) and the seedling absent group (Figure 3), and low scores associated with moss or litter substrate (Table 1) and both the seedling present and seedling missing groups (Figure 3).

These results were confirmed by a series of univariate one-way analyses of variance (ANOVA) that tested each substrate variable across all three seedling groups (Table 2). Seedling absent plots had significantly greater percent tussock substrate (mean

= 76%) than either seedling present plots (mean = 3%) or seedling missing plots (mean = 3%; Table 2). The univariate ANOVAs showed that the mean percent cover of both moss and litter substrate were significantly lower for the seedling absent group than for the other seedling groups (Table 2).

Examination of the second discriminant function (DF2) showed that seedlings were more likely to be found at elevations within 30 cm of the water table than at higher elevations on hummocks with moss-litter substrate. Elevation relative to water table was the only predictor on DF2 with a large standardized canonical discriminant function coefficient (0.9, Table 1). High scores on this function were associated with greater elevations while low scores were associated with lower elevations. Points with high scores on DF2 and thus high scores on elevation were predicted to be in the seedling missing group (Figure 3).

Again, the one-way analyses of variance reinforced the multivariate results as the mean elevation of seedling missing plots was significantly greater (mean = 33.9) than the elevations of the seedling present (mean = 17.6) or seedling absent plots (mean = 19.0, Table 2). Elevation was clearly a predictor of seedling presence at Brown Mill Pond. A larger number of plots with cedar seedlings was located at low to intermediate elevations (10-25 cm) than at either the lowest (< 5 cm) or highest (> 30 cm) elevations on hummocks with moss-litter substrate (Figure 4a). While plots were less common at elevations less than 10 cm, all four of these plots contained cedar seedlings (Figure 4b).

According to the discriminant analysis, several environmental predictors did not strongly contribute to either discriminant function. Percent open canopy and herb and

Table 2. The group mean for each predictor variable used in a standard discriminant analysis that tested the predictability of Atlantic white-cedar seedling group membership at Brown Mill Pond, Rye, New Hampshire (July 2000). Standard deviations are reported in parentheses. F and p values are for the main effect of one-way analyses of variance comparing a predictor variable across all 3 seedling classification groups. Means with the same letter are not significantly different according to a Tukey's multiple comparison test ($p < 0.05$).

| | Classification Group Mean | | | | |
|---|---|---|---|---|---|
| Predictor Variable | Seedling Present (n=57) | Seedling Missing (n=57) | Seedling Absent (n=57) | F | p |
| Elevation Relative to Water Table (cm) | 17.61a (5.30) | 33.91b (8.47) | 19.01a (9.32) | 74.77 | < 0.001 |
| % Open Canopy | 10.39a (3.32) | 8.28b (2.38) | 11.71a (3.78) | 16.49 | < 0.001 |
| % Moss Substrate | 35.14a (26.89) | 20.21b (24.04) | 2.25c (6.14) | 34.66 | < 0.001 |
| % Litter Substrate | 47.26a (30.26) | 74.79b (28.44) | 10.96c (28.47) | 69.11 | < 0.001 |
| % Tussock Substrate | 3.32a (17.35) | 3.53a (15.98) | 76.33b (38.15) | 150.59 | < 0.001 |
| Herb and Shrub Density | 2.93a (6.53) | 4.46a (9.08) | 51.11b (38.11) | 81.29 | < 0.001 |
| Distance to Nearest Parent Tree (cm) | 64.61a (59.31) | 82.55a (101.55) | 203.02b (102.39) | 39.84 | < 0.001 |

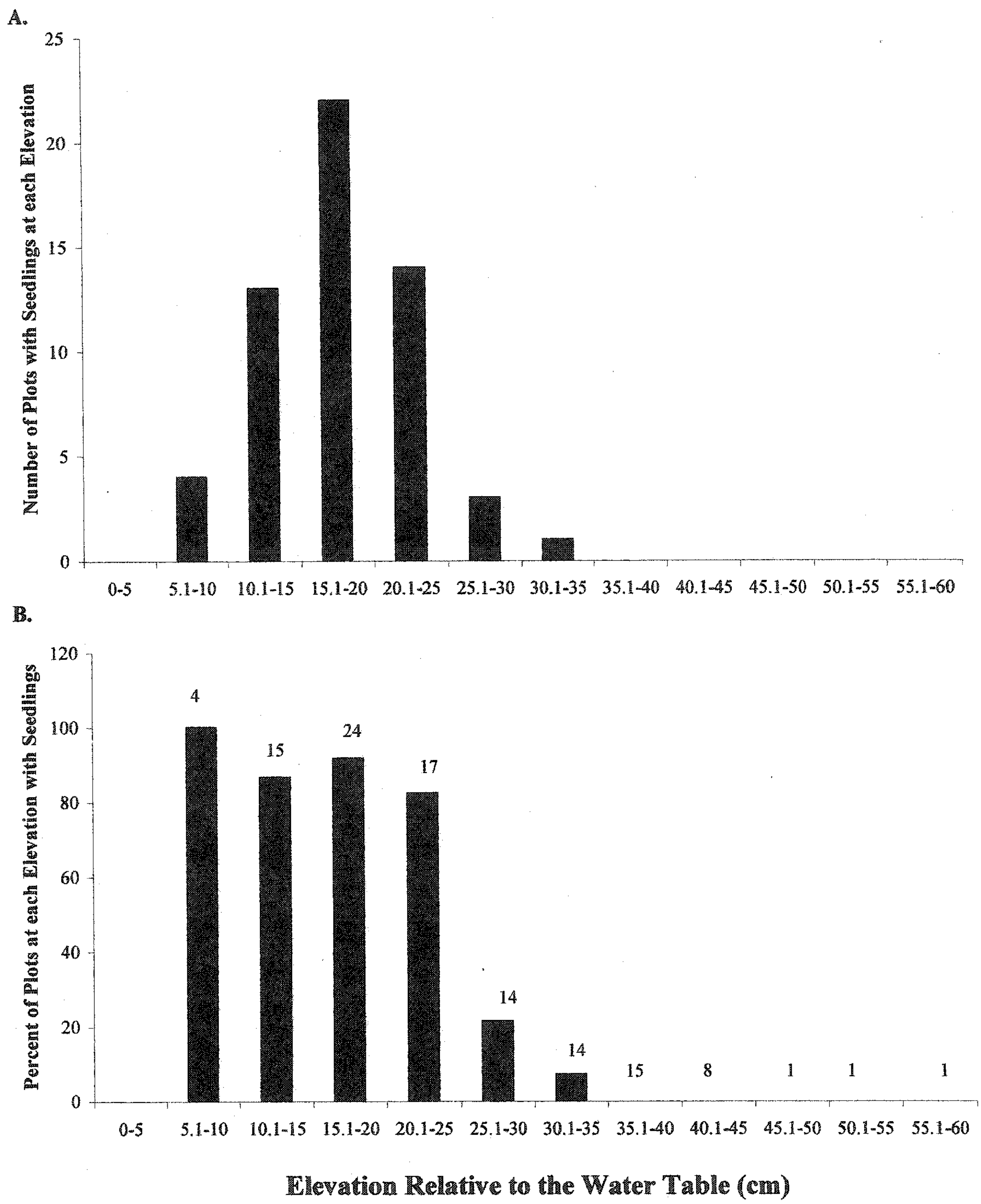



Figure 4. Results of Atlantic white-cedar seedling survey conducted in the pond edge community at Brown Mill Pond, Rye, New Hampshire. **A.** The number of plots with cedar seedlings for each elevation class on moss-litter hummocks. Elevations were adjusted to a single water table height in July (7/3/00). **B.** Percent of plots at each elevation with cedar seedlings. Number above elevations gives sample size of that class.

shrub density had the lowest standardized canonical discriminant function coefficients and therefore were not strongly associated with either discriminant function (Table 1). Distance to nearest parent tree had a moderate coefficient (0.356) on DF1, but this predictor was not considered a strong contributor as all the substrate predictors had larger coefficients ($\geq$ 0.378).

In summary, the discriminant analysis demonstrated that seedlings were absent from hummocks with tussock sedge substrate and present on hummocks with some alternative substrate (e.g., moss or leaf litter). On moss-litter hummocks, seedlings were present at low to intermediate elevations (10-25 cm) relative to the water table while missing from the highest elevations (> 30 cm).

**Regression Analysis**

The overall multiple regression of seedling number per hummock on hummock area and substrate was statistically significant [Figure 5, $R^2 = 0.40$, $F = 17.60$, df = 3, $p < 0.001$, $Y' = 1.1663 + 0.024(\text{sqrt area}) - 0.6781(\text{substrate type}) - 0.0058(\text{sqrt area x substrate type})$]. Only one of the independent variables contributed significantly to prediction of number of seedlings per hummock. Specifically, square root of hummock area had a standardized regression coefficient that differed significantly from zero ($\beta = 0.68$, $t = 2.15$, $p = 0.03$, Table 3) while coefficients associated with substrate type and the interaction did not differ significantly from zero ($p > 0.05$, Table 3). Mean area of moss-litter hummocks was 1.104 $m^2$, while mean area of tussock sedge hummocks was 0.349 $m^2$.

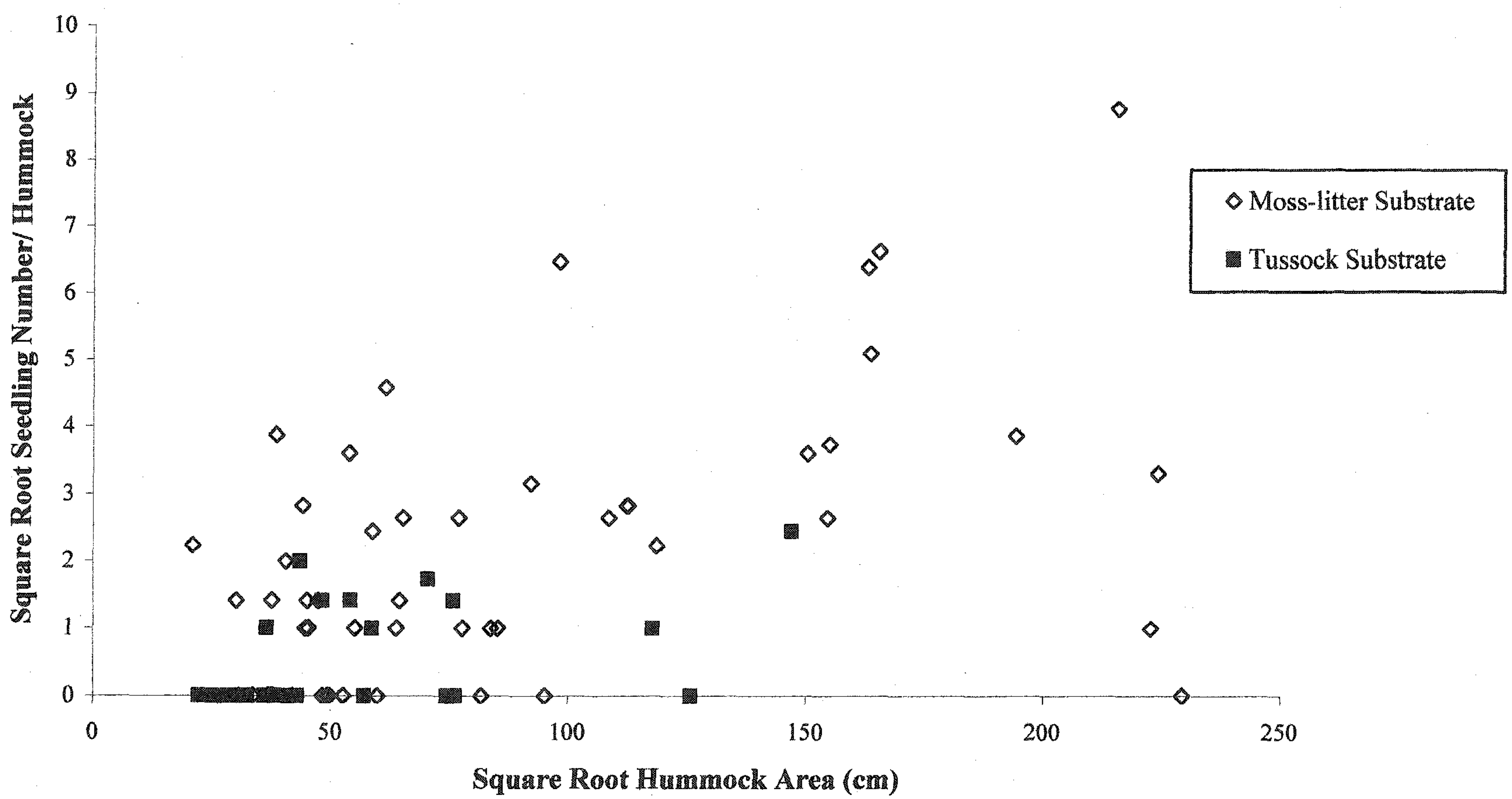



Figure 5. Scatterplot illustrating the linear relationship between hummock area and Atlantic white-cedar seedling number per hummock at Brown Mill Pond, Rye, New Hampshire (July 2000). Data were square root transformed prior to analysis. Hummocks with moss-litter substrate and tussock substrate were included.

Table 3. Results of standard multiple regression performed between Atlantic white-cedar seedling number per hummock as the dependent variable and hummock substrate type, area, and their interaction as the independent variables at Brown Mill Pond, Rye, New Hampshire (July 2000). Hummock area and seedling number were square root transformed prior to analysis.

| Independent Variable | Unstandardized Coefficient (b) | Standardized Coefficient (β) | t-ratio | p |
|---|---|---|---|---|
| Square Root of Hummock Area | 0.024 | 0.682 | 2.15 | 0.03 |
| Hummock Substrate Type | -0.678 | -0.178 | -1.08 | 0.29 |
| Sqrt Area x Substrate Type | -0.006 | -0.188 | -0.63 | 0.53 |
| Constant | 1.1663 | 0 | 1.29 | 0.20 |

## Discussion

### Overall Pattern of Cedar Seedling Distribution at Brown Mill Pond

Cedar seedling distribution was not random at Brown Mill Pond. Seedlings were absent from hummocks with tussock sedge (*Carex stricta*) substrate and present on hummocks with some alternative substrate such as moss or leaf litter. On the moss-litter hummocks, seedlings were present most often 10-25 cm above the water table and missing from the highest elevations (> 30 cm).

### Substrate Type

As similarly determined in a recent field survey and greenhouse experiments conducted by Allison and Ehrenfeld (1999), cedar seedlings in this study preferred a peat-based substrate with overlying moss or litter more than a graminoid-based substrate with overlying sedge and grass. Historically, organic peat has been considered a suitable site for cedar seedlings (Little 1950). Little (1950) reported that these soils are generally acidic (pH 3.5-5.5). With the exception of Allison and Ehrenfeld (1999), few cedar seedling surveys have investigated the distribution of established seedlings in relation to soil type. Although germination studies alone may not determine long-term establishment requirements, as seeds may germinate in microsites that later prove unsuitable for long-term survival (Allison and Ehrenfeld 1999), greenhouse experiments indicate stronger germination on peat moss than sand (Zimmermann 1993). According to Mylecraine and Zimmermann (2000), the factor explaining this difference in germination is still unknown, although pH and moisture holding capacity have been ruled out. Although cedar seedlings appear to grow best in peat substrate, sphagnum moss, moist mineral soil, and rotten wood have also been reported as suitable cedar seedbeds (Laderman 1989, Mylecraine and Zimmermann 2000).

There are three hypotheses that may explain the lack of cedar establishment on tussock hummocks relative to moss-litter hummocks at Brown Mill Pond. First, elevation relative to the water table may differ between the two types of hummocks. However, the elevations of tussock hummocks (mean $\text{elevation}_{\text{seedling absent}} = 19.01$ cm above the water table) were very similar to the elevations that were considered most suitable for establishment on moss-litter hummocks (mean $\text{elevation}_{\text{seedling present}} = 17.61$ cm above the water table) at Brown Mill Pond (Figure 3 and Table 2).

Second, it is possible that the tussock substrate itself may be unsuitable for cedar germination and growth. Perhaps the texture or pH of tussock hummocks is unsuitable for cedar germination or establishment. These questions were specifically tested in subsequent field experiments (Chapter II), which showed germination and growth can occur on tussocks (Gengarelly, unpublished data).

A third hypothesis is that the lack of cedar on tussocks may be due to the relatively small size of tussock hummocks, which on average were 32% as large as moss-litter hummocks. Wind-dispersed cedar seed is more likely to encounter a larger hummock than a small one. A multiple regression analysis including hummock substrate type and hummock area offered support for this hypothesis, as substrate was not a significant predictor of seedling number per hummock when hummock area was included in the model (Figure 5 and Table 3). This analysis overall only explained 40% of the variance in seedling number per hummock, so hummock area may only partially explain the lack of seedlings on tussocks at Brown Mill Pond.

**Elevation Relative to the Water Table**

At Brown Mill Pond, seedlings were less likely to occur at the lowest and highest elevations of the moss-litter hummocks. The average difference between highest points (hummock tops) and lowest points (hollows or bottoms) in the pond edge community at Brown Mill Pond was 52 cm ± 7, with a maximum difference of 85 cm (Gengarelly 1999). Most seedlings were found at a low to intermediate elevation relative to the water table (10-25 cm above an approximately 22 cm water table or 32-47 cm above the hollow surface). Similar to the pattern at Brown Mill Pond, Ehrenfeld (1995b) suggested that cedar seedlings were absent from lowest microsites, especially the bottom 20 cm of hummocks relative to the hollow surface, studied in New Jersey. In fact, a band of cedar seedlings at the intermediate zone was reported in New Jersey by Ehrenfeld (1995b, personal communication 2001) in sites where hummock height was large enough to include an intermediate elevation (~ 35-55 cm above the hollow surface). Similarly, Akerman (1923) indicated cedar survival was best at the mid-section of rotting stumps, though he did not indicate if these elevations were relative to the water table or hollow surface.

It has been suggested that microtopography, as it affects moisture availability, may be an important factor explaining cedar seedling distribution on hummocks (Ehrenfeld 1995a and 1995b). The lack of seedlings in the hollows is attributed to frequent flooding in these depressions (Allison and Ehrenfeld 1999, Mylecraine and Zimmermann 2000). In fact, wetland woody species in general establish on elevated microsites, avoiding standing water (Huenneke and Sharitz 1990, Titus 1990). The lack of seedlings at the highest elevations of hummocks at Brown Mill Pond corresponds to cedar's requirement for sufficient moisture for survival (Little 1950, Allison and Ehrenfeld 1999). Insufficient moisture has been associated with inadequate germination and reduced seedling growth (Little 1950).

**Other Factors**

The multivariate analysis indicated that neither density of competing plants nor percent canopy cover played a strong determining role in cedar seedling distribution. While univariate tests indicated that all variables signficantly differed across all seedling groups, the univariate tests were not as robust because unlike the multivariate test they did not control for the variance accounted for by the other variables.

Previous research offers conflicting evidence regarding competing vegetation and light requirements (Buell and Cain 1943, Little 1950, Korstian and Brush 1931, Hickman and Neuhauser 1977, Motzkin 1990, Mylecraine and Zimmermann 2000). According to Buell and Cain (1943) open seed beds free of competing vegetation in North Carolina were optimal for cedar establishment (Buell and Cain 1943). However, Korstian and Brush (1931) found that seedlings become established under the shade of shrubs. The present survey was conducted in the pond edge community at Brown Mill Pond where light is not likely limited. In this area of the wetland the canopy is not closed and peripheral diffuse illumination from the open space above the pond may contribute to the understory light regime. In this case, light levels may have been high enough throughout the study area that factors such as competing vegetation abundance and percent open sky had minimal effect on seedling distribution. The light regime in the pond edge community was unique and not found elsewhere in the wetland. Light was probably more limited in the other communities at Brown Mill Pond (Figure 1), perhaps explaining the lack of cedar seedlings in these areas of the swamp (Gengarelly 1999).

Herbivory may also limit seedling presence and absence in certain parts of cedar's geographic range. In New Jersey, in particular, deer browse has contributed to great losses of cedar seedling presence in many wetlands (Kuser and Zimmermann 1995). Although herbivory was not quantified in this survey, herbivory appears to be rare or uncommon at Brown Mill Pond because surveyed individuals did not demonstrate browse. This does not imply that herbivore pressure will not be a factor in seedling distribution patterns in the future.

Distance to the nearest prospective parent tree was not as strong a factor as elevation and substrate in determining cedar seedling presence at Brown Mill Pond, though it had the next highest discriminant function coefficient to these variables (Table 1). Perhaps the proximity of seed source was not as important as other factors because the pond edge canopy was dominated by both Atlantic white-cedar and red maple (*Acer rubrum*; Gengarelly 1999). However, in a study that compared six wetlands, Allison and Ehrenfeld (1999) suggest that cedar establishment was associated with a cedar canopy that serves as a dependable cedar seed source. If a disturbance, such as fire, removed much of the existing juvenile and adult cedars from Brown Mill Pond, then distance to nearest parent tree may become an important factor in establishment given that the seed bank was unviable.

In general, disturbance (e.g., windthrow, commercial harvesting, fire, drought, or flooding) is expected to alter the available habitats in a wetland. For instance, extensive drought during the growing season may permit seedling establishment in the lowest elevations, typically areas devoid of seedlings due to standing water (Allison and Ehrenfeld 1999). Ehrenfeld (1995b) showed that sites with a history of more frequent windthrow had taller hummocks and the distribution of tree seedlings, including cedar, shifted to slightly higher elevations in these wetlands. Thus, if Brown Mill Pond experiences a disturbance in the near future, then the current seedling distribution patterns are likely to change.

## Conclusion

This study describes the microsite conditions associated with the cedar seedling distribution at Brown Mill Pond. Specifically, cedar seedlings occurred in scattered clumps on moss-litter hummocks typically 10-25 cm above the water table. Seedlings were absent from tussock sedge hummocks; however, tussock sedge hummocks were smaller than moss-litter hummocks. These patterns suggested that seedling distribution may be directly controlled by moisture as a function of elevation and edaphic conditions associated with different substrates. However, these relationships are just associations and only field experiments that rigorously test the exact microhabitat conditions will determine the causal factors in cedar establishment.

## CHAPTER II

## THE ROLE OF MICROTOPOGRAPHY AND SUBSTRATE IN ATLANTIC WHITE-CEDAR SEEDLING EMERGENCE AND GROWTH

### Abstract

One reason for the decline of Atlantic white-cedar populations may be unsuccessful seedling recruitment in existing wetlands. Consequently, there has been much recent interest in cedar's recruitment requirements and in techniques for regenerating and restoring cedar populations. This study used field experiments to examine cedar seedling establishment in an uneven-aged stand at Brown Mill Pond, Rye, New Hampshire. The experiments evaluated emergence (germination and early seedling growth) and second year seedling survival and growth with respect to two principal factors identified in a previous field survey: (1) elevation relative to the water table and (2) substrate type.

In the *elevation-moisture experiment*, native cedar seeds were sown at equal densities in November 2001 at different elevations on hummocks. The elevation-moisture experiment was a multi-factor experiment including elevation [i.e., "intermediate" (17-22 cm above the water table) and "high" (35-40 cm above the water table)] and supplemental watering (i.e., with and without) as the main treatments. In the single factor *substrate type experiment*, seeds were sown into either "moss-litter" or "tussock sedge" substrate. These plots were monitored bi-monthly for a single growing

season (2002) and the number of emerged seedlings was quantified. The identical experimental design was used to quantify the effects of elevation relative to water table and substrate type on the establishment, growth, and survival of greenhouse-grown, second year Atlantic white-cedar seedlings transplanted to the field. Seedlings were monitored over two growing seasons (2001 and 2002) and changes in seedling height, branch number, stem diameter, and above ground biomass were quantified. In order to describe potentially important physical conditions associated with each treatment, I measured the following environmental variables within each treatment of the experiments: soil pH, soil redox potential, soil temperature, air temperature, and soil moisture.

Elevation above the water table reflected a moisture and pH gradient on moss-litter hummocks at Brown Mill Pond and, as expected from the previous seedling distribution survey (Chapter I), small-scale variation in elevation affected cedar seedling performance and establishment. Total number of emerged seedlings was lowest in the high elevation-not watered treatment. Furthermore, second year individuals growing in the high elevation-not watered treatment were characterized by the lowest growth in height, branch number, and biomass as well as the greatest mortality. Cedar seedling emergence, establishment, growth, and survival at high elevations increased when seedlings were watered. In contrast to expectations based on the seedling distribution survey, there was only a weak substrate type effect on seedling emergence and performance. Substrate type had little if any effect on seedling emergence and second year seedling growth. These results, together with those of the field survey (Chapter I), suggested that moisture and associated factors influenced cedar recruitment at Brown Mill Pond, while hummock substrate did not.

## Introduction

Since colonial times Atlantic white-cedar populations have declined in size and number. This decline has occurred throughout the species' already restricted range along the eastern coast of the United States (Laderman et al. 1987, Motzkin 1990, Sperduto and Ritter 1994, Sheffield et al. 1998). Some of these losses have been attributed to inadequate recruitment under a closed canopy and subsequent successional change (Korstian and Brush 1931, Little 1950, Hickman and Neuhauser 1977, Motzkin 1990, Stoltzfus and Good 1998). A closed cedar canopy, however, may not be the primary limiting factor to cedar establishment (Kuser and Zimmermann 1995). In fact, reports are conflicting concerning the shade tolerance of Atlantic white-cedar (Korstian and Brush 1931, Little 1950, Hickman and Neuhauser 1977, Motzkin 1990, Stoltzfus and Good 1998). Other limiting factors, observed at a microhabitat scale, including microtopography, soil moisture, and substrate, may better explain the lack of successful cedar recruitment in some wetlands (Ehrenfeld 1995b, Allison and Ehrenfeld 1999).

As remaining populations of cedar are confined to conservation lands, the decline of cedar due to inadequate recruitment of cedar seedlings has become an important management concern (Motzkin 1990, Kuser and Zimmermann 1995, Allison and Ehrenfeld 1999, Mylecraine and Zimmermann 2000). In fact, there has been much recent interest in cedar's recruitment requirements and techniques for regenerating and restoring cedar populations (Ehrenfeld 1995b, Kuser and Zimmermann 1995, Mylecraine and Zimmerman 2000). Most of the cedar seedling research has been conducted in New

Jersey and is based on seedling distribution surveys and some greenhouse and field experiments (Little 1950, Ehrenfeld 1995b, Zimmermann 1997, Allison and Ehrenfeld 1999, Haas and Kuser 1999).

New Hampshire cedar seedling distribution trends were undetermined until I conducted a field survey at Brown Mill Pond in Rye, New Hampshire (Chapter I). Unlike the majority of the even-aged, monospecific, Atlantic white-cedar wetlands in the northern portion of cedar's range (Sperduto and Ritter 1994, Stockwell 1999), Brown Mill Pond demonstrated natural regeneration. Successful cedar establishment was found in an uneven-aged stand, the *pond edge community*, adjacent to the brook and pond (Gengarelly 1999). The pond edge community was distinguished by a discontinuous cedar-red maple canopy and the highest water table in the site (Gengarelly 1999, Chapter III). This non-light limited community provided an unusual opportunity to study the biological and physical conditions associated with cedar seedling recruitment on hummocks in a New Hampshire wetland (Chapter I).

One result of the Brown Mill Pond field survey was the identification of two types of hummocks based on the dominant surface substrate: tussock sedge and moss-litter hummocks. Tussock sedge hummocks were characterized by tussock sedge (*Carex stricta*) substrate, which consisted of a network of vertical rhizomes intertwined with plant detritus, such as dead roots and leaf litter (Lord and Lee 2001). Moss-litter hummocks were characterized by patches of bryophytes, primarily mosses including *Sphagnum* spp., *Dicranum* spp., and other taxa, interspersed with areas covered with leaf and twig litter. These moss-litter hummocks are commonly described in other cedar wetlands and referred to simply as "peat hummocks" or sometimes as "litter-covered hummocks" (Laderman 1989, Ehrenfeld 1995a, Mylecraine and Zimmermann 2000). According to the Brown Mill Pond survey, the distribution of cedar seedlings on the tussock sedge and moss-litter hummocks was non-random, with seedlings absent from tussock sedge hummocks and present on moss-litter hummocks (Chapter I).

In accordance with the pattern found at Brown Mill Pond, other studies of cedar seedlings have shown greater frequency of occurrence or growth in organic peat soils (i.e., histosols) with moss and litter substrate than on other substrates (Little 1950, Laderman 1989, Allison and Ehrenfeld 1999). Field observations have shown a greater abundance of cedar in peat with a litter substrate (Little 1950) than in mineral soil (Mylecraine and Zimmermann 2000) or in peat with a graminoid substrate (Allison and Ehrenfeld 1999). Greenhouse experiments have indicated that cedar grows better in peat than a *Sphagnum* mat (Allison and Ehrenfeld 1999). However, Haas and Kuser (1999) found it was possible to establish cedar seedlings on a sandy mineral soil. These conflicting results illustrate that there is still uncertainty in our understanding of cedar germination and seedling establishment requirements with regard to substrate. As yet, field experiments that test substrate type as a limiting factor of cedar germination or establishment have not been conducted.

The Brown Mill Pond survey also showed that cedar seedlings were most common at "intermediate" elevations on hummocks, 10-25 cm above the water table, and were less common at higher elevations on these hummocks, which reached heights of up to 60 cm above the water table (Chapter I). This finding is also consistent with other studies (Ehrenfeld 1995b, Mylecraine and Zimmermann 2000). It has been suggested that microtopography, especially as it affects moisture availability, may be an important factor explaining cedar seedling distribution on hummocks (Korstian and Brush 1931; Little 1950; Ehrenfeld 1995a, 1995b). According to Ehrenfeld (1995b), cedar seedlings were most common at intermediate elevations and avoided the lowest and highest elevations of hummocks in a New Jersey wetland. Seedling recruitment may have been unsuccessful at the top of hummocks and at the lowest elevations in the hollows because of drought and prolonged flooding respectively. According to Kuser and Zimmermann (1995), field observations have indicated that moisture is the primary limiting factor influencing cedar establishment, with too much or too little water being detrimental to seedling survival.

Each stage in a plant's life history may represent a bottleneck for successful recruitment and thereby may regulate seedling distribution (DeSteven 1991a). As dispersal is an unlikely bottleneck in cedar seedling recruitment (Korstian and Brush 1931, Kuser and Zimmermann 1995), seedling germination and establishment success, collectively referred to here as "emergence", were assessed in this study. Until now emergence and early growth of seedlings have not been compared in the field.

Field surveys are correlative in nature and lack the rigor of field experiments that test a particular factor's effect on seedling growth and survival. In order to determine the factors underlying cedar seedling distribution at Brown Mill Pond, field experiments were designed and initiated during the 2001 field season. These field experiments tested the factors identified in the field survey—substrate type and elevation relative to the water table—in order to explain cedar recruitment in the pond edge community at Brown Mill Pond. Seeds and seedlings were used to evaluate seedling emergence, survival, and growth with respect to substrate type and elevation relative to the water table. Specifically, the following questions were addressed in this investigation:

1a. What is the effect of elevation above water table on cedar seedling emergence and to what extent is this effect modified by supplemental watering?

1b. Does cedar seedling emergence vary between tussock sedge and moss-litter substrate?

2a. What is the effect of elevation above water table on the survival and growth of second year cedar seedlings and to what extent are these effects modified by supplemental watering?

2b. Does survival and growth of second year cedar seedlings vary between tussock sedge and moss-litter substrate?

## Methods

### Field Experiments- germination and seedling emergence

Experimental Design Experiments were designed to quantify the effects of elevation relative to water table and substrate type on Atlantic white-cedar germination and first year establishment. The experiments were conducted in the pond edge community at Brown Mill Pond (for a description of the study area see Chapter I methods).

Two seedling experiments were designed: a two-factor elevation-moisture experiment and a single factor substrate type experiment. The *elevation-moisture experiment* tested the following two factors: elevation relative to the water table and supplemental watering. The elevation factor had two levels: "intermediate" (17-22 cm above the water table) and "high" (35-40 cm above the water table). These elevations were established in the field by measuring the current water table depth and adjusting these measurements to those obtained July 3, 2000. In this way, all elevations on hummocks were relative to the July 2000 water table and these represented the appropriate elevations to be tested based on the seedling distribution survey (Chapter I). Supplemental watering involved two levels: watered and not watered. Watered plots were watered three times a week throughout the 2002 growing season with water from Brown Mill Pond (i.e., "pond water") until soil within 15 cm of plots was saturated. All four possible combinations of the two factors were tested. The second experiment (i.e., *substrate type experiment*) compared seedling emergence on two kinds of substrate: tussock sedge and moss-litter substrate.

Germination-seedling emergence experiments were initiated in November 2001 as peak Atlantic white-cedar seed dispersal occurs in late autumn (e.g., October-November, Korstian and Brush 1931). Each experiment was a completely randomized design with 10 replicates for each treatment. Each hummock was an experimental unit (i.e., a replicate). Hummocks were randomly selected and then assigned to one of the treatments. Each replicate included two 10 x 10 cm control plots and two 10 x 10 cm experimental plots. Plots were marked by wooden dowels and flagging. Each replicate received a total 160 cedar seeds (i.e., 80 seeds/ plot; seeds collected September-

November 2001 on site) while accompanying control plots received none. Control plots were used to measure baseline cedar emergence densities. All plots were monitored twice a month (June-August 2002) and the number of seedlings per plot was quantified.

In order to determine if changes in cedar emergence over time differed by treatment, a series of simple linear regressions were performed. Each regression used one of the two response variables (e.g., % plots with seedling emergence or total # of emerged seedlings) as the dependent variable and time (i.e., date of measurement) as the independent variable. Separate regressions were performed for each treatment factor. In order to determine whether the slopes of these regression lines were significantly different within a particular experiment (e.g., elevation-moisture experiment), an analysis of co-variance (ANCOVA) was used. This tested a response variable (e.g., % plots with seedling emergence) across experimental treatments and included the date of measurement as the covariate. In this analysis, a significant interaction term, treatment x date, indicated significant differences among the slopes. A multicomparison test, equivalent to a Tukey test, was used to compare more than two slopes (Zar 1996). ANCOVA and regressions were performed using SYSTAT 5.2 (Wilkinson et al. 1992) while the multicomparison test was calculated by hand using a procedure outlined by Zar (1996).

**<u>Field Experiments-2$^{nd}$ year seedlings</u>**

The identical experimental design was used to quantify the effects of elevation relative to water table and substrate type on the establishment, growth, and survival of second year Atlantic white-cedar seedlings. In the second year seedling experiments each replicate included six cedar seedlings.

All seedlings were propagated from the Brown Mill Pond seed pool. Cedar cones and seeds were collected in seed traps in October and November 1999. Seeds were stored in glass vials in a cool dry place over the winter. In the spring, 1,800 seeds were sent to Arrowwood Nursery Inc. in Williamstown, New Jersey, for propagation. Cedar seeds were planted in peat soil and once seedlings were 2.5 cm tall they were fertilized and weeded each month (C. Arensault, personal communication; May 2001). In June, 2001, when seedlings were in their second growing season and 5 to 15 cm tall, they were sent overnight to Durham, New Hampshire.

All seedlings were separated and planted with remaining peat on the same day (June 8, 2001) in appropriate treatments which had been previously flagged. Holes were dug such that each seedling was planted no more than 0.5 cm above its original soil level. Commercial peat moss was used to fill in around seedling root systems so that no roots were exposed. Seedlings were marked with aluminum tags. Each seedling was protected from herbivory by rigid seedling protector tubes (polyethylene-polypropylene diamond mesh 1" wide; 3.25" in diameter and 12" length) staked in place with bamboo sticks. Immediately following transplanting each seedling was watered with pond water until soil within 15 cm of the seedling was saturated (~ 8-16 liters/ replicate).

Maintenance In order to ensure initial transplant success, all seedlings were watered with pond water three times a week during the first month (8 June-8 July). Furthermore, during this period seedlings were lightly fertilized twice with a dilute foliar spray [i.e., 1/4 teaspoon or 0.89 g Miracle Grow (15-30-15 N-P-K ratio & micronutrients) to eight liters tap water] to minimize the stress of transplanting. After three weeks of supplemental watering, watering was continued only in the treatments of the elevation-moisture experiment that required it. Replicates of these treatments were watered generally three times a week throughout the 2001 and 2002 growing seasons (~June-October).

Measurements Approximately a week before general watering ended (i.e., 4 July - 8 July 2001), the following variables were measured for each seedling: initial height (mm ruler), branch number, and stem diameter (digimatic micrometer, Mitutoyo Inc.). Dry aboveground biomass was considered an important growth measure, but it was impossible to directly determine the initial dry biomass of transplanted seedlings. Thus, to estimate dry biomass from other variables, 45 haphazardly chosen seedlings were measured for height and stem diameter. This subsample of seedlings was then sacrificed to determine dry aboveground biomass; each seedling was weighed following 48 hours in a 100 °C oven (Chapman 1976). Biomass of these seedlings was regressed on height and stem diameter (see Statistical Analyses section, below). This equation was then used to estimate the dry aboveground biomass of each of the transplanted seedlings.

Seedling survival was monitored monthly during the 2001 and 2002 field seasons (~June-October). Final seedling growth measurements were taken in September 2002. In addition to measuring height, branch number, and stem diameter, seedlings were harvested for the dry biomass assessment.

The following growth measures were calculated for each seedling: *absolute* change in seedling height, seedling branch number, seedling stem diameter, and dry aboveground biomass, as well as *percent* change in height, branch number, stem diameter, and biomass [e.g., ($\Delta$ in height/ initial height )* 100]. All of these calculations represented the difference between final and initial measurements, except for dry biomass measures whose initial values were based on an estimate (see Statistical Analyses section, below). All calculations were based on non-transformed data, including biomass calculations that used back-transformed $\log_e$ biomass estimates to determine change in biomass for each seedling.

To obtain values for each replicate, I pooled the growth measures for the six seedlings per replicate. Thus, the mean of the six seedlings was used in all subsequent statistical analyses. In the end, survival, mean absolute seedling growth, and percent seedling growth per treatment were used as the response variables.

Reference Seedlings At the beginning of the seedling experiments, a random sample of 40 naturally established seedlings was selected (five/ transect) for growth measurements (height, branch #, and stem diameter). Any cedar displaying some scale-like foliage and a height $\geq 5$ and $< 30$ cm was considered a seedling. These seedlings were measured at the same time as the experimental seedlings and used as a reference for "background" growth rates.

Statistical Analyses Estimation of the initial biomass of each experimental seedling was accomplished with a multiple linear regression using initial measurements of the 45 "sacrificed" seedlings. Biomass was the response variable while seedling height and stem diameter were the explanatory variables. A linear model was tested first, followed by a $\log_e$ model that transformed both the response (i.e., biomass) and explanatory variables (i.e., height and diameter).

Analysis of variance (ANOVA) was used to analyze the mean absolute and percent seedling growth data (e.g., change in height, percent change in dry biomass) across the appropriate experimental treatment(s). In the elevation-moisture experiment, a two-way ANOVA was used to test each mean absolute or percent growth measure across both treatments plus an interaction term (i.e., elevation x watering). Each test that produced a statistically significant interaction term was followed by a Tukey multiple comparison test. A one-way ANOVA was performed on substrate type experiment data and tested for differences in growth measures across the two soil types. Differences in final biomass were compared across treatments using analysis of co-variance (ANCOVA), which included as covariates the initial growth measures (i.e., initial height, branch number, and stem diameter). This test was performed with $\log_e$ biomass data. All statistical analyses were performed using SYSTAT 5.2 (Wilkinson et al. 1992).

**Environmental Variables**

In order to describe some of the potentially important physical conditions associated with each treatment, the following environmental variables were measured within each treatment of the experiments: soil pH, soil redox potential, soil temperature, air temperature, and soil water content.

Measurements All environmental parameters were measured the day following supplemental watering or precipitation. Soil pH and redox potential were measured according to standard techniques (Chapman 1976) with a digital pH/redox meter (SmartStick, AST Inc.). On both overcast and cloudless days soil and air temperatures were obtained with a digital thermometer (Taylor Inc.) that was either set to a 5 cm soil depth or held 5 cm above the soil surface and left for one minute to equilibrate.

Soil water content was measured according to the gravimetric method (Slatyer 1970). Initial soil samples (i.e., one per replicate) were obtained the day following precipitation. Surface soil (peat) was taken from the appropriate elevation of each replicate. Soil was collected in tared aluminum soil tins (4 oz) that were sealed with tape, labeled and transported to lab. Samples were weighed wet the same day and then dried at 105 °C for 3 days and weighed again. Water content was calculated based on the mass of these soil samples and expressed as mass of water per unit mass of dry soil. After several days (e.g., 1 week) without precipitation, soil was collected again to evaluate how water content changed in each treatment over a period of dry weather.

All environmental variables were evaluated twice during the 2001 growing season. At each time of measurement two readings per replicate were obtained for soil pH, soil redox potential, soil temperature, and air temperature. These two readings were averaged to obtain a single value per replicate ($n = 10$). Thus, the average environmental measures were based on ten estimates. Soil moisture was evaluated in July and August. July measurements were cut short by unexpected precipitation. Thus, only the August measurements were analyzed, as these involved a full week without precipitation (i.e., August 21 -28, 2001). The redox meter was considered faulty and was replaced mid-season. Consequently, one set of redox measurements were analyzed.

<u>Statistical Analyses</u> Analysis of variance (ANOVA) was used to analyze the above environmental data across the appropriate experimental treatment(s) for each time of measurement. In the elevation-moisture experiment, a two-way ANOVA was used to test each average environmental measure across both treatments. Each test that produced a statistically significant interaction term was followed by a Tukey multiple comparison test. A one-way ANOVA was performed on substrate type experiment data and tested for differences in average environmental measures across the two substrate types. All statistical analyses were performed using SYSTAT 5.2 (Wilkinson et al. 1992).

## Results

### Field Experiments- germination and seedling emergence

Control Plots Many of the control plots were contaminated by sown seeds from the adjacent treatment plots as seeds moved more easily than expected over distances of 10 cm. Flooded conditions in June 2002 were likely responsible for the lateral movement of seeds. Therefore, controls were rejected as an indicator of baseline cedar emergence densities in this study because the "true" number of contaminated control plots was unknown.

Elevation-Moisture Experiment Originally I intended to analyze the number and percent of plots with emerged seedlings per replicate (via ANOVA) in order to determine the mean differences in seedling emergence across treatments. However, emergence rates were low and the large number of plots with no emerged seedlings precluded the use of ANOVA. Consequently, I pooled all replicates per treatment in order to calculate the total number of emerged seedlings and the percentage of replicates with emerged seedlings per treatment and observation.

The percentage of plots with seedling emergence significantly differed among the elevation-moisture treatments over time ($F_{\text{treatmnt x date}} = 21.6$, df=3, $p < 0.001$). In the high elevation-not watered treatment, percentage of plots with emerged seedlings declined from June (80%) to August (30%) while in all other treatments it increased or stabilized (Tukey test's critical value $q > 4.529$, $k = 4$, df = 8, $p < 0.05$; Figure 6). In contrast to the high elevation-not watered treatment, high elevation-watered plots started with 80% of the plots with emerged seedlings and, in late August, 70% of plots still had emerged cedar seedlings (Figure 6). Furthermore, the percent of intermediate elevation

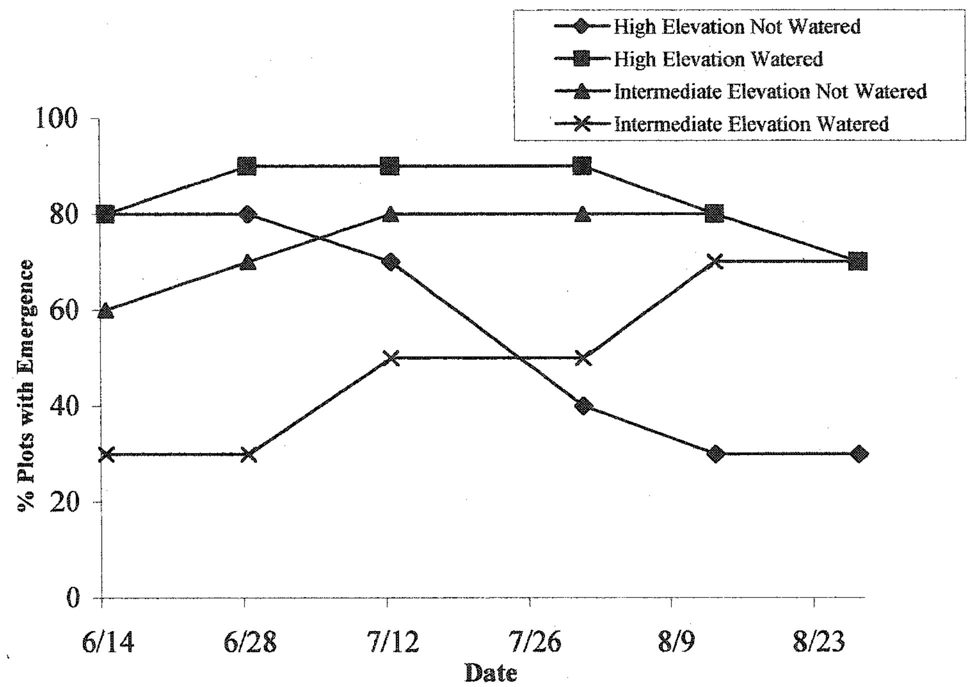



Figure 6. Percent of plots with Atlantic white-cedar emergence across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire June 14 to August 27, 2002 (n = 10).

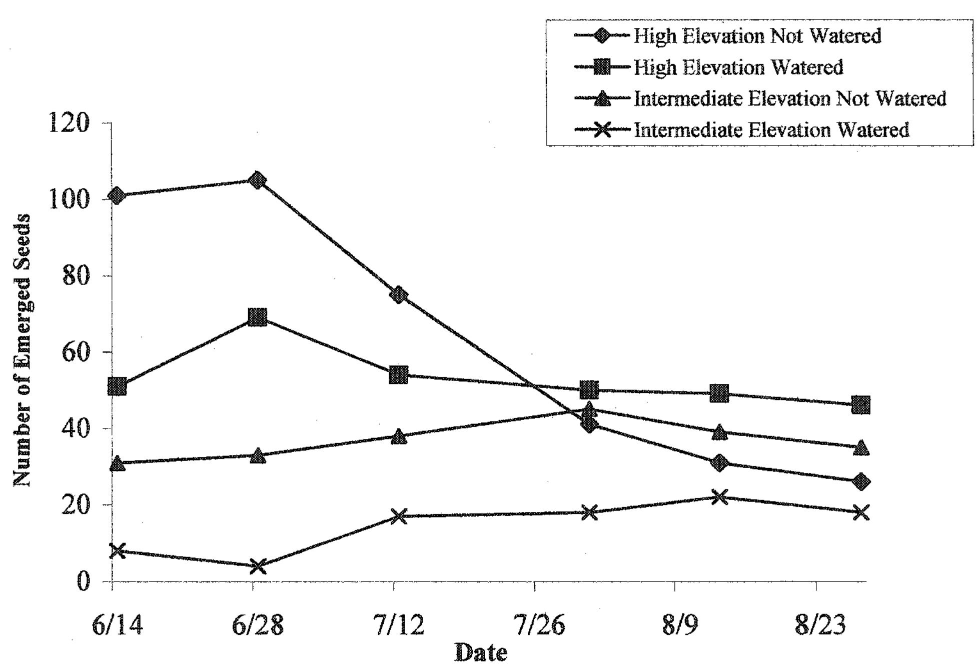



Figure 7. Total number of emerged Atlantic white-cedar seedlings across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire June 14 to August 27, 2002.

plots with emerged seedlings in early June ranged from 30%-60% depending on the watering regime and in late August 70% of each of these intermediate elevation treatment plots contained emerged seedlings (Figure 6).

A similar pattern was found in the total number of emerged seedlings among the elevation-moisture treatments over time. Overall, emerged seedlings located at high elevation-not watered treatment declined from June (101 seedlings) to August (26 seedlings) while emerged seedlings in all the other treatments increased and/or stabilized at similar values (Figure 7). Again, seedling emergence differed significantly among the elevation-moisture treatments over time ($F_{\text{treatmnt x date}} = 23.9$, $df = 3$, $p < 0.001$) and the high elevation-not watered treatment significantly differed from all other treatments (Tukey test's critical value $q > 6.9$, $k = 4$, $df = 8$, $p < 0.005$).

Substrate Type Experiment In general, cedar seedling emergence was greater in moss-litter substrate compared to that on tussock sedge substrate. However, by the end of the growing season, differences were less pronounced. In early June, 100% of moss-litter plots and 20% of tussock sedge plots contained emerged seedlings. In late August, 60% of the moss-litter plots still contained emerged seedlings while 40% of tussock sedge plots had emerged seedlings (Figure 8). The decline in percent of moss-litter plots with emerged seedlings was significantly different from the moderate increase and stabilization in percentage of tussock sedge plots with seedling emergence ($F_{\text{treatmnt x date}} = 30.5$, $df = 1$, $p < 0.0001$).

The total number of emerged seedlings in each substrate type followed a similar trend. Moss-litter plots initially contained a greater number of total emerged seedlings

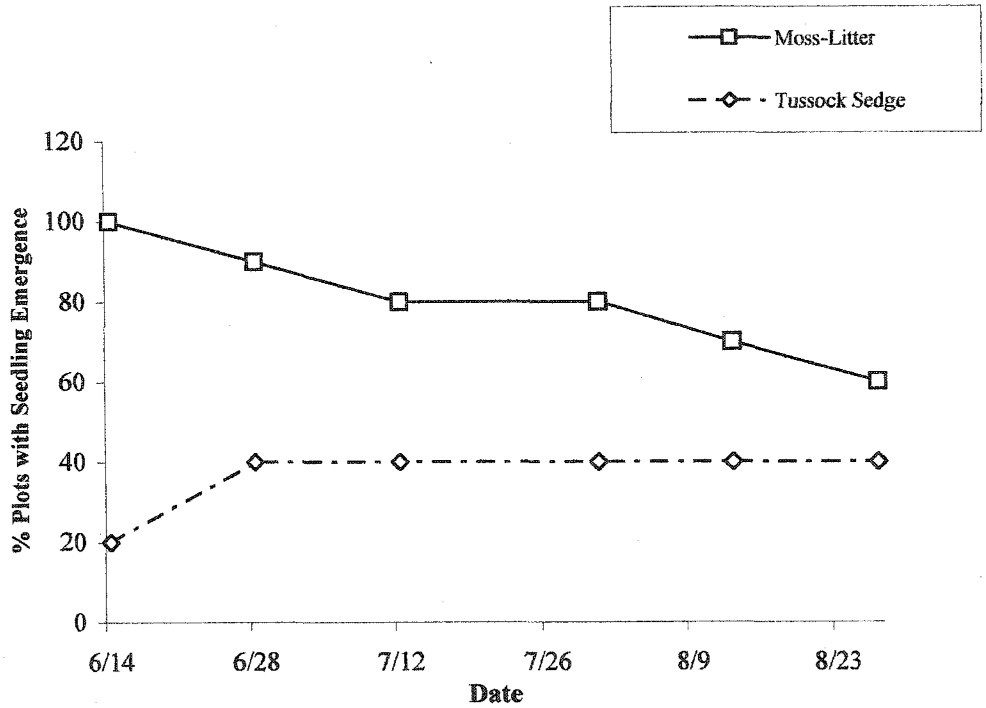



Figure 8. Percent of plots with Atlantic white-cedar emergence in each substrate treatment at Brown Mill Pond, Rye, New Hampshire June 14 to August 27, 2002 (n = 10).

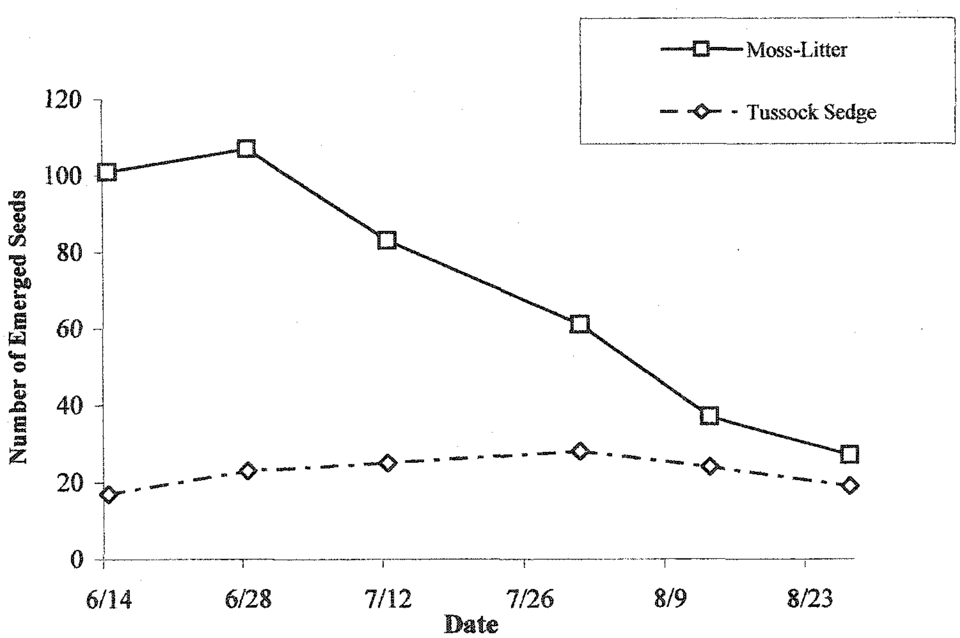



Figure 9. Total number of emerged Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire June 14 to August 27, 2002.

(100) than tussock sedge plots (17). Over time, the number of seedlings declined in the moss-litter plots while the number of seedlings in the tussock sedge plots only varied moderately. At the end of August, moss-litter plots had a total of 27 emerged seedlings while tussock sedge plots had a total of 19 (Figure 9). These trends were significantly different ($F_{treatmnt\ x\ date} = 52.1$, df =1, $p < 0.0001$).

**<u>Field Experiments-2nd year seedlings</u>**

<u>Biomass Estimation</u> To assess seedling growth, initial seedling biomass had to be determined. The regression equation used to estimate initial biomass of all seedlings was $\log_e$ biomass = -5.13 + 1.29($\log_e$ height) + 1.02($\log_e$ stem diameter). This predictive equation explained more variance ($R^2 = 0.77$, F = 68.8, df = 2 , $p < 0.05$) than the regression equation based on non-transformed data ($R^2 = 0.71$, F = 53.0, df = 2 , $p < 0.05$).

<u>Elevation-Moisture Experiment</u> Ninety-five percent of the experimental seedlings (229 of 240) survived. Eight of the 11 seedlings that died were located in the high elevation-not watered treatment and these individuals were distributed among half of the plots in that treatment (Table 4). Seedling mortality within the high elevation-not watered treatment was 13% and ranged from 0% to only 3% in the three other treatments (Table 4).

In general, cedar seedlings grew less in the high elevation-not watered treatment than in the other three treatments (Figures 10-15). The final biomass of seedlings growing in the high elevation-not watered treatment (0.43 g) was significantly less than that of seedlings in all other treatments (~ 0.60 g; $F_{elev\ x\ water} = 4.1$, df = 1, $p \leq 0.05$; Figure 10, Table 5). In fact, seedlings located in the high elevation-not watered treatment only

Table 4. Mortality of Atlantic white-cedar seedlings in the elevation-moisture experiment implemented at Brown Mill Pond, Rye, New Hampshire (July 2001-September 2002).

| **Treatment** | **Total Mortality** | **% Seedling Mortality** | **# Plots with Mortality** | **% Plots with Mortality** |
|---|---|---|---|---|
| High Elevation, not Watered | 8 | 13 | 5 | 50 |
| High Elevation, Watered | 2 | 3 | 2 | 20 |
| Intermediate Elevation, not Watered | 1 | 2 | 1 | 10 |
| Intermediate Elevation, Watered | 0 | 0 | 0 | 0 |

Table 5. Results of ANCOVA testing final Atlantic white-cedar seedling biomass at Brown Mill Pond, Rye, New Hampshire, in 2002 across elevation and watering treatments and including the initial growth measures as covariates.

| **Source of Variation** | **df** | **SS** | **MS** | **F** | **p** |
|---|---|---|---|---|---|
| Total | 39 | 2.249 | | | |
| Elevation | 1 | 0.306 | 0.306 | 7.0 | 0.01 |
| Watered | 1 | 0.153 | 0.153 | 3.5 | 0.07 |
| Elevation*watered | 1 | 0.179 | 0.179 | 4.1 | 0.05 |
| Initial Height | 1 | 0.086 | 0.086 | 2.0 | 0.17 |
| Initial Branch # | 1 | 0.052 | 0.052 | 1.2 | 0.28 |
| Initial Stem Diameter | 1 | 0.028 | 0.028 | 0.6 | 0.43 |
| Error | 33 | 1.445 | 0.044 | | |

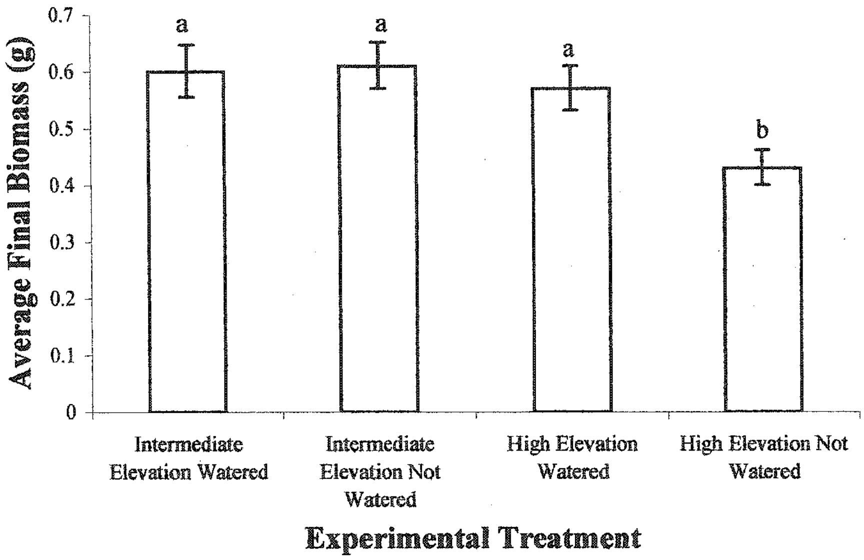



Figure 10. Mean final biomass of Atlantic white-cedar seedlings across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire (September 2002). Means with the same letter are not significantly different as a result of analysis of covariance and Tukey's multiple comparison test ($\alpha = 0.05$). Error bars represent standard error.

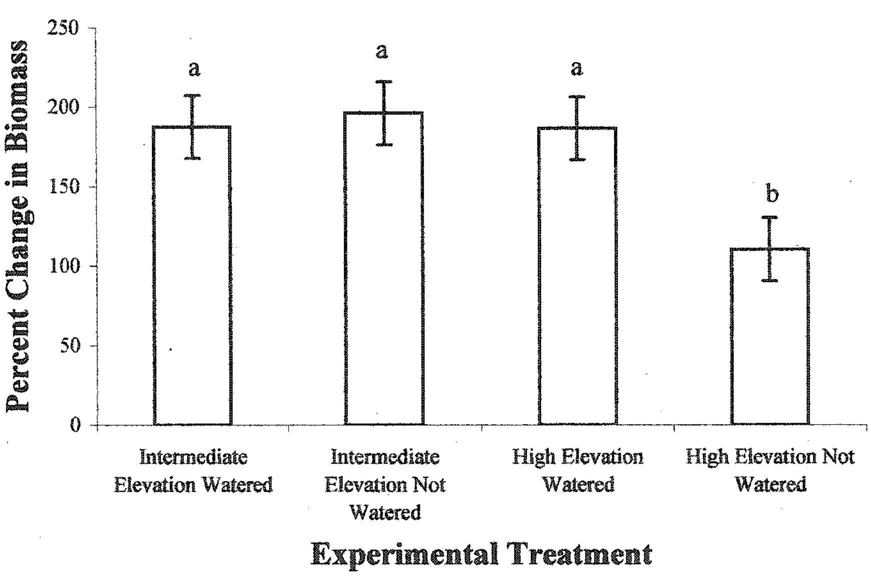



Figure 11. Mean percent change in biomass of Atlantic white-cedar seedlings across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance and Tukey's multiple comparison test ($\alpha = 0.05$). Error bars represent standard error.

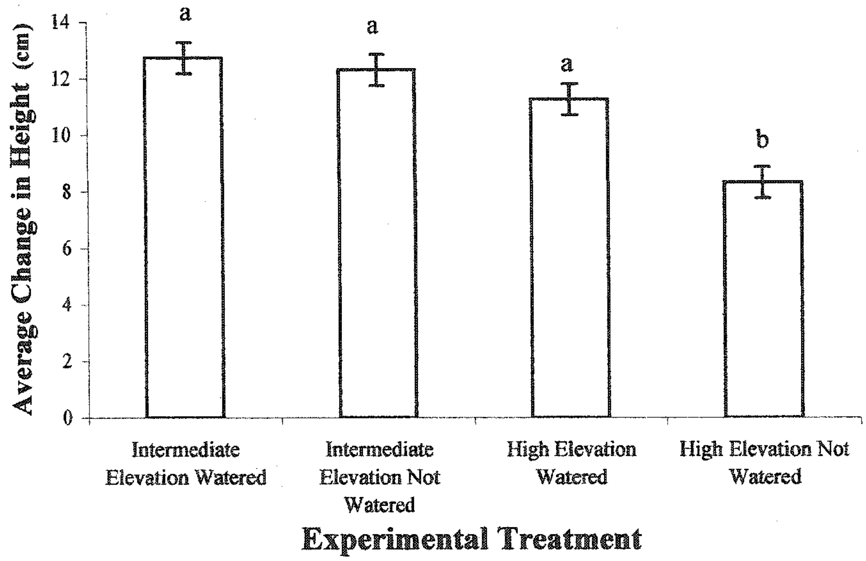



Figure 12. Mean change in height of Atlantic white-cedar seedlings across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance and Tukey's multiple comparison test ($\alpha = 0.05$). Error bars represent standard error.

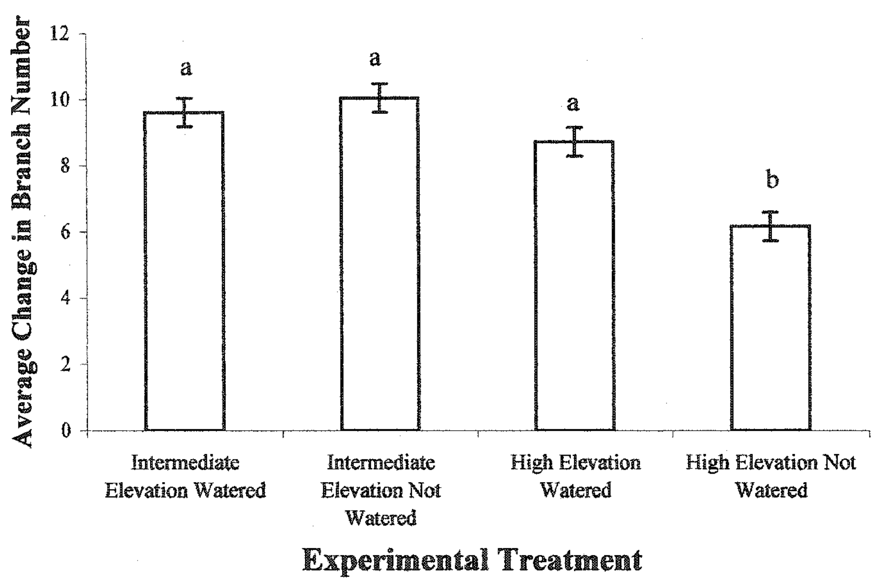



Figure 13. Mean change in branch number of Atlantic white-cedar seedlings across all elevation-water treatments at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance and Tukey's multiple comparison test ($\alpha = 0.05$). Error bars represent standard error.

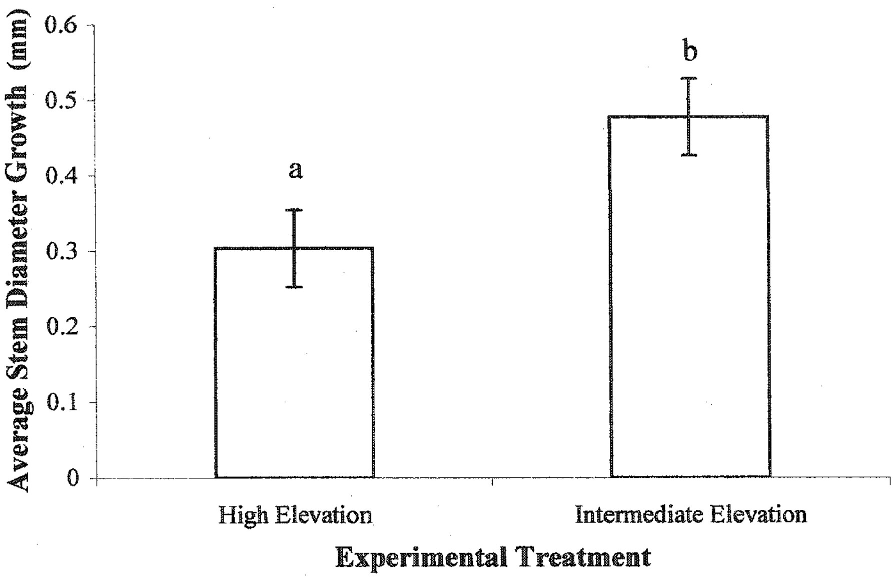



Figure 14. Mean change in stem diameter of Atlantic white-cedar seedlings across each elevation treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

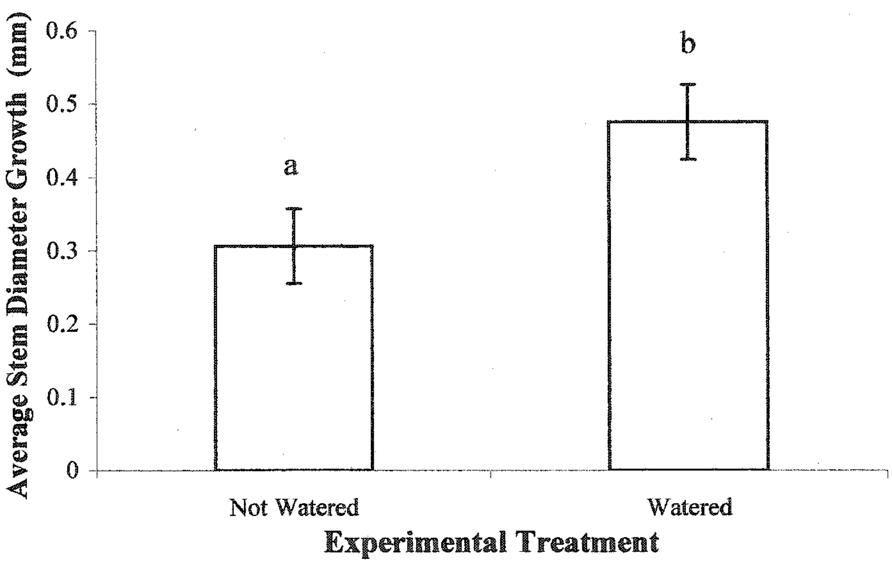



Figure 15. Mean change in stem diameter of Atlantic white-cedar seedlings across each water treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

Table 6. Results of ANOVA testing the growth of Atlantic white-cedar seedlings in each treatment of the elevation-moisture experiment implemented in Rye, NH (7-01 to 9-02).

| Source of Variation | df | SS | MS | F | p |
|---|---|---|---|---|---|
| **A.** *% increase in Biomass* | | | | | |
| Elevation | 1 | 18922.9 | 18922.9 | 4.8 | 0.04 |
| Watered | 1 | 11412.6 | 11412.6 | 2.9 | 0.10 |
| Elevation*watered | 1 | 17949.2 | 17949.2 | 4.6 | 0.04 |
| Error | 36 | 141840.6 | 3940.0 | | |
| **B.** *Absolute increase in height* | | | | | |
| Elevation | 1 | 74.4 | 74.4 | 24.7 | 0.0001 |
| Watered | 1 | 28.4 | 28.4 | 9.4 | 0.004 |
| Elevation*watered | 1 | 15.8 | 15.8 | 5.2 | 0.03 |
| Error | 36 | 108.3 | 3.0 | | |
| **C.** *Absolute increase in branch #* | | | | | |
| Elevation | 1 | 57.1 | 57.1 | 30.8 | 0.0001 |
| Watered | 1 | 11.4 | 11.4 | 6.1 | 0.018 |
| Elevation*watered | 1 | 22.5 | 22.5 | 12.1 | 0.001 |
| Error | 36 | 66.7 | 1.9 | | |
| **D.** *Absolute increase in stem diameter* | | | | | |
| Elevation | 1 | 0.3 | 0.3 | 5.8 | 0.02 |
| Watered | 1 | 0.3 | 0.3 | 5.6 | 0.02 |
| Elevation*watered | 1 | 0.1 | 0.1 | 1.7 | 0.19 |
| Error | 36 | 1.9 | 0.1 | | |
| **E.** *% increase in height* | | | | | |
| Elevation | 1 | 4950.6 | 4950.6 | 12.2 | 0.001 |
| Watered | 1 | 2544.0 | 2544.0 | 6.3 | 0.02 |
| Elevation*watered | 1 | 1550.0 | 1550.0 | 3.8 | 0.05 |
| Error | 36 | 14644.3 | 406.8 | | |
| **F.** *% increase in branch #* | | | | | |
| Elevation | 1 | 3097.6 | 3097.6 | 12.0 | 0.001 |
| Watered | 1 | 828.1 | 828.1 | 3.2 | 0.08 |
| Elevation*watered | 1 | 1768.9 | 1768.9 | 6.9 | 0.01 |
| Error | 36 | 9275.8 | 257.7 | | |
| **G.** *% increase in stem diameter* | | | | | |
| Elevation | 1 | 652.9 | 652.9 | 4.1 | 0.05 |
| Watered | 1 | 715.7 | 715.7 | 4.5 | 0.04 |
| Elevation*watered | 1 | 452.93 | 452.93 | 2.9 | 0.10 |
| Error | 36 | 5677.1 | 157.7 | | |

doubled in biomass (i.e., increase of ~100%) while all other seedlings tripled in biomass (i.e., increase of ~ 200%; $F_{elev\ x\ water} = 4.6$, df = 1, $p \leq 0.05$; Figure 11, Table 6a). Furthermore, the increase in height (8.32 vs. ~ 12.1 cm increase in height; $F_{elev\ x\ water} = 5.2$, df = 1, $p \leq 0.05$; Figure 12, Table 6b) and branch number (6.2 vs. ~ 9.5 increase in branch #; $F_{elev\ x\ water} = 12.1$, df = 1, $p \leq 0.001$; Figure 13, Table 6c) of these high elevation-not watered seedlings were significantly less than that of seedlings in all other treatments. Seedling stem diameter was significantly less for all individuals growing at high elevations than at intermediate elevations regardless of the watering regime ($F_{elev} = 5.8$, df = 1, $p \leq 0.05$; Figure 14, Table 6d) and for all seedlings lacking watering regardless of elevation relative to the water table ($F_{water} = 5.6$, df = 1, $p \leq 0.05$; Figure 15, Table 6d).

Percent increase in seedling height, branch number, and stem diameter followed the same trends described above for the corresponding absolute measure of these variables (Tables 6e-g).

Substrate Type Experiment In the substrate type experiment, only one seedling located in tussock sedge substrate died (Table 7). All other seedlings survived the two growing seasons (2001 and 2002).

Overall, growth was greater for seedlings located in tussock sedge substrate compared to those grown in moss-litter substrate. Although final biomass of seedlings grown in tussock sedge (0.76 g) and moss-litter substrate (0.66 g) was not significantly different ($F_{sub\ type} = 3.5$, df = 1, $p > 0.05$; Figure 16, Table 8), percent increase in biomass was greater in tussock sedge substrate (228%) than in moss-litter substrate (168%; $F_{sub}$

Table 7. Mortality of Atlantic white-cedar seedlings in substrate type experiment implemented at Brown Mill Pond, Rye, New Hampshire (July 2001-September 2002).

| Treatment | Total Mortality | % Seedling Mortality | # Plots with Mortality | % Plots with Mortality |
|---|---|---|---|---|
| Moss-Litter Substrate | 0 | 0 | 0 | 0 |
| Tussock Substrate | 1 | 2 | 1 | 10 |

Table 8. Results of ANCOVA testing final Atlantic white-cedar seedling biomass at Brown Mill Pond, Rye, New Hampshire, in 2002 across substrate treatments and including the initial growth measures as covariates.

| Source of Variation | df | SS | MS | F | p |
|---|---|---|---|---|---|
| Total | 19 | 0.693 | | | |
| Substrate Type | 1 | 0.098 | 0.098 | 3.5 | 0.08 |
| Initial Height | 1 | 0.047 | 0.047 | 1.7 | 0.22 |
| Initial Branch # | 1 | 0.129 | 0.129 | 4.6 | 0.05 |
| Initial Stem Diameter | 1 | 0.000 | 0.000 | 0.0 | 0.99 |
| Error | 15 | 0.419 | 0.028 | | |

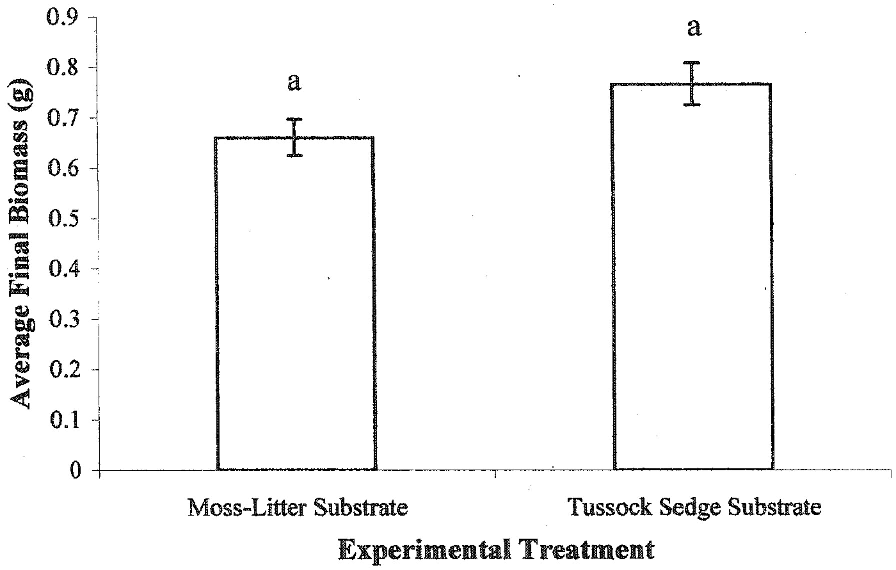



Figure 16. Mean final biomass of Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire (September 2002). Means with the same letter are not significantly different as a result of analysis of covariance ($\alpha = 0.05$). Error bars represent standard error.

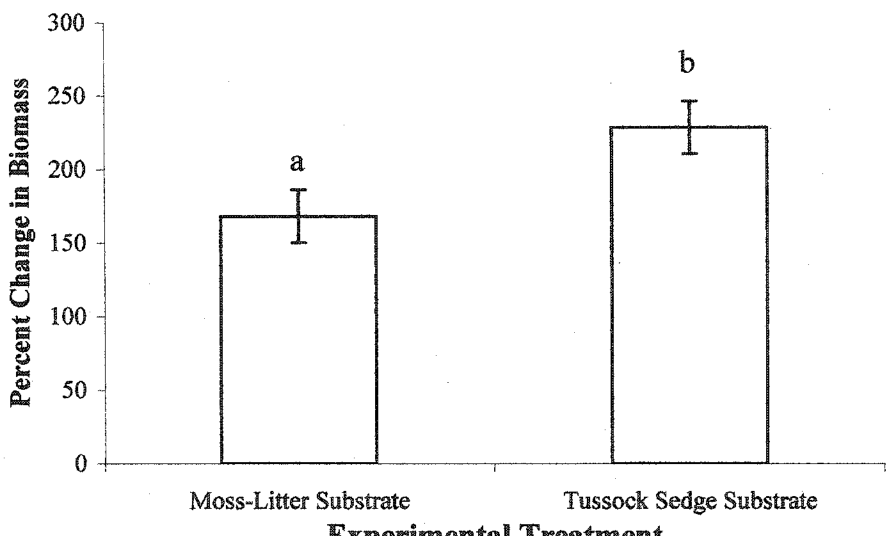



Figure 17. Mean percent change in biomass of Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

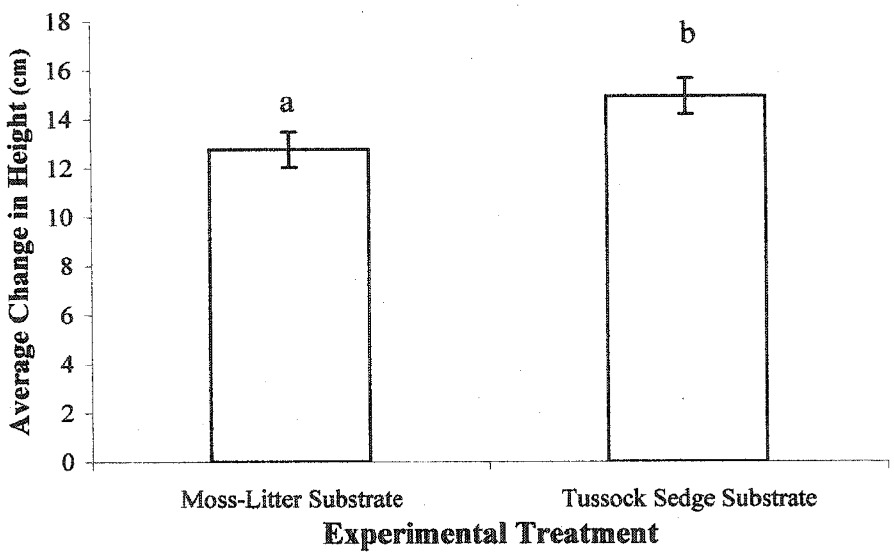



Figure 18. Mean change in height of Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

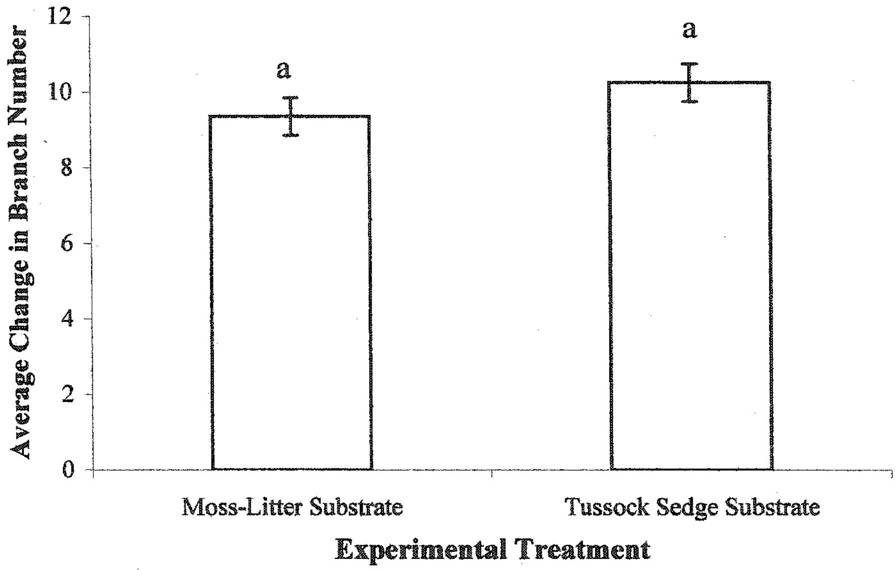



Figure 19. Mean change in branch number of Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

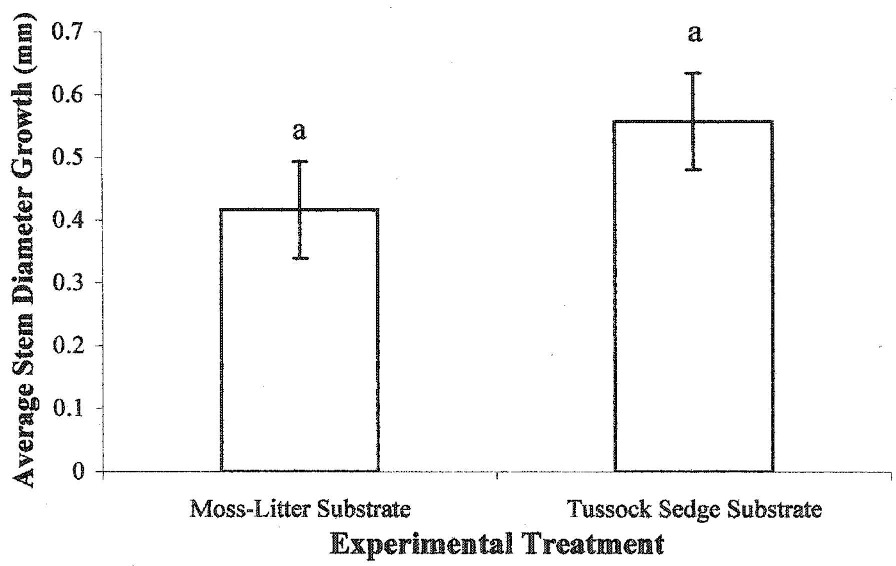



Figure 20. Mean change in stem diameter of Atlantic white-cedar seedlings in each substrate treatment at Brown Mill Pond, Rye, New Hampshire (June 2001 to September 2002). Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$). Error bars represent standard error.

Table 9. Results of ANOVA testing the growth of Atlantic white-cedar seedlings from 2001 to 2002 in each treatment of the substrate type experiment implemented at Rye, New Hampshire.

| Source of Variation | df | SS | MS | F | p |
|---|---|---|---|---|---|
| **A.** *% increase in biomass* | | | | | |
| Substrate Type | 1 | 18189.7 | 18189.7 | 5.7 | 0.03 |
| Error | 18 | 57911.4 | 3217.3 | | |
| **B.** *Absolute increase in height* | | | | | |
| Substrate Type | 1 | 23.1 | 23.1 | 4.4 | 0.05 |
| Error | 18 | 95.2 | 5.3 | | |
| **C.** *Absolute increase in branch #* | | | | | |
| Substrate Type | 1 | 4.1 | 4.1 | 1.7 | 0.22 |
| Error | 18 | 44.2 | 2.5 | | |
| **D.** *Absolute increase in stem diameter* | | | | | |
| Substrate Type | 1 | 0.1 | 0.1 | 1.7 | 0.21 |
| Error | 18 | 1.1 | 0.059 | | |
| **E.** *% increase in height* | | | | | |
| Substrate Type | 1 | 1748.5 | 1748.5 | 3.6 | 0.08 |
| Error | 18 | 8787.3 | 488.2 | | |
| **F.** *% increase in branch #* | | | | | |
| Substrate Type | 1 | 104.4 | 104.4 | 0.4 | 0.54 |
| Error | 18 | 4794.9 | 266.4 | | |
| **G.** *% increase in stem diameter* | | | | | |
| Substrate Type | 1 | 262.8 | 262.8 | 1.7 | 0.20 |
| Error | 18 | 2729.2 | 151.6 | | |

Table 10. Growth measures for natural reference and experimental Atlantic white-cedar seedlings of the elevation-water and substrate experiments implemented at Brown Mill Pond, Rye, New Hampshire (June 2001-September 2002). Average values reported with standard errors reported in parentheses. Only maximum and minimum average values among treatments and standard errror within that treatment reported for experimental seedlings.

| | Average Change in Height (cm) | Average Change in Branch Number | Average Change in Stem Diameter (mm) | Relative Change in Height (%) | Relative Change in Branch Number (%) | Relative Change in Stem Diameter (%) |
|---|---|---|---|---|---|---|
| Natural Reference Seedlings | 1.98 (0.22) | 1.3 (0.3) | 0.191 (0.029) | 20.1 (2.1) | 26.0 (1.8) | 12.9 (5.7) |
| Maximum Value of Elevation-Water Experiment | 12.73 (0.55) | 10.0 (0.4) | 0.477 (0.051) | 127.1 (6.4) | 90.2 (5.1) | 25.6 (2.8) |
| Minimum Value of Elevation-Water Experiment | 8.32 (0.55) | 6.2 (0.4) | 0.303 (0.051) | 88.9 (6.4) | 59.3 (5.1) | 17.4 (2.8) |
| Maximum Value of Substrate Type Experiment | 14.90 (0.73) | 10.3 (0.5) | 0.557 (0.077) | 147.1 (7.0) | 90.6 (5.2) | 29.0 (3.9) |
| Minimum Value of Substrate Type Experiment | 12.75 (0.73) | 9.4 (0.5) | 0.416 (0.077) | 128.4 (7.0) | 86.0 (5.2) | 21.7 (3.9) |

$_{type} = 5.7$, df = 1, $p \leq 0.05$; Figure 17, Table 9a). Furthermore, the increase in height of seedlings located in tussock sedge substrate (14.9 cm) was greater than seedlings in moss-litter substrate (12.7 cm; $F_{sub\ type} = 4.3$, df = 1, $p \leq 0.05$; Figure 18, Table 9b). Seedling branch number ($F_{sub\ type} = 1.7$, df = 1, $p > 0.05$; Figure 19, Table 9c) and stem diameter ($F_{sub\ type} = 1.7$, df = 1, $p > 0.05$; Figure 20, Table 9d) did not differ significantly between the substrate types.

Percent increases in seedling height, branch number, and stem diameter did not differ significantly between the substrate types (Table 9e-g).

Reference Seedlings The naturally established "reference" seedlings had slower growth rates than experimental seedlings in either experiment. During the sampling period, the increases in height and branch number of experimental seedlings were at least four times greater than that of reference seedlings (Table 10). Moreover, experimental seedlings' growth in stem diameter was on average two times greater than that of reference seedlings (Table 10).

**Environmental Variables Per Treatment**

Elevation-Moisture Experiment The soil in high elevation-not watered plots contained less moisture than all other treatments. Specifically, after a week without precipitation the high elevation-not watered plots lost significantly more moisture (-39.4%; $F_{elev\ x\ water} = 10.7$, df = 1, $p < 0.01$) and were characterized by significantly lower soil moisture (~1 g $H_2O$/ g dry soil) than all other treatments (~ 3-5 g $H_2O$/ g dry soil; $F_{elev\ x\ water} = 43.0$, df = 1, $p < 0.001$; Table 11).

Mean air temperature in overcast conditions during the first observation (i.e., August 17, 2001) was slightly though significantly greater at the higher elevations (21.7

°C) than at the intermediate elevations (21.4 °C; $F_{elev} = 11.4$, df = 1, $p < 0.01$; Table 12) while watering made no significant difference in temperature ($F_{water} = 0.3$, df = 1, $p > 0.05$). In contrast, mean air temperature did not significantly differ among elevation-water treatments on cloudless days during the first and second observations ($F_{elev\ x\ water}$ = 0.03 and 0.06 respectively, df = 1, $p > 0.05$) or in overcast conditions during the second observation ($F_{elev\ x\ water} = 1.8$, df = 1, $p > 0.05$). Soil temperatures did not differ significantly among the elevation-watered treatments on overcast days ($F_{elev\ x\ water}$ = 0.01-0.3, df = 1, $p > 0.05$) or cloudless days ($F_{elev\ x\ water}$ = 1.1-0.06, df = 1, $p > 0.05$) during either observation date (Table 12).

In general, the soil was more acidic (pH = 4.10) in high elevation plots than intermediate elevation plots (pH = 4.68) during the first observation, July 11, 2001, just days following the end of general watering ($F_{elev} = 33.40$, df =1, $p < 0.001$). During the second observation (e.g., August 22, 2001) the soil was more acidic in high elevation-not watered treatment (pH = 3.89) than all other treatments (pH ≈ 4.6-4.8; $F_{elev\ x\ water} = 13.5$, df = 1, $p < 0.01$; Table 11).

Soil redox potential differed among the watered treatments regardless of elevation. Watered plots had a significantly lower redox potential (446 mV) than those that lacked supplemental watering (486 mV; $F_{water} = 5.0$, df = 1, $p < 0.05$; Table 11). Soil redox potential did not differ significantly among elevation treatments ($F_{elev} = 1.8$, df =1, $p > 0.05$; Table 11).

Substrate Type Experiment The tussock sedge plots had significantly greater soil moisture (~ 5 g $H_2O$/ g dry soil) than the moss-litter plots (~ 4 g $H_2O$/ g dry soil; $F_{sub\ type} = 6.0$, df = 1, $p < 0.05$; Table 13). After a week without precipitation this trend held and

Table 11. The mean values for several environmental variables across all treatments of the elevation-moisture experiment implemented at Brown Mill Pond Atlantic white-cedar wetland in Rye, New Hampshire (2001). The mean value for each environmental variable is reported plus or minus the standard error. Means with the same letter are not significantly different as a result of analysis of variance and Tukey's multiple comparison test ($\alpha = 0.05$).

| Environmental Variable | Elevation | Not Watered | Watered |
|---|---|---|---|
| Soil Moisture after One Week without Rain ($g\ H_2O/\ g$ dry soil) | High | $1.14^{a} \pm 0.18$ | $2.91^{b} \pm 0.18$ |
| | Intermediate | $4.84^{c} \pm 0.18$ | $4.22^{c} \pm 0.18$ |
| % Change in Soil Moisture after One Week without Rain | High | $-39.4^{a} \pm 8.3$ | $3.5^{b} \pm 8.3$ |
| | Intermediate | $6.5^{b} \pm 8.3$ | $-4.7^{b} \pm 8.3$ |
| pH (July 11, 2001) | High | $4.10^{a} \pm 0.07$ | $4.10^{a} \pm 0.07$ |
| | Intermediate | $4.68^{b} \pm 0.07$ | $4.68^{b} \pm 0.07$ |
| pH (August 22, 2001) | High | $3.89^{a} \pm 0.14$ | $4.63^{b} \pm 0.14$ |
| | Intermediate | $4.83^{b} \pm 0.14$ | $4.56^{b} \pm 0.14$ |
| Redox Potential (mV) | High | $486^{a} \pm 13$ | $446^{b} \pm 13$ |
| | Intermediate | $486^{a} \pm 13$ | $446^{b} \pm 13$ |

Table 12. The mean air and soil temperatures across all treatments of the elevation-moisture experiment implemented at Brown Mill Pond Atlantic white-cedar wetland in Rye, New Hampshire (2001). Observation I and II obtained in overcast conditions (August 17 and 20 respectively) and cloudless conditions (July 20 and 30 respectively). The mean value for each temperature is reported plus or minus the standard error. Means with the same letter are not significantly different as a result of analysis of variance and Tukey's multiple comparison test ($\alpha = 0.05$).

| Environmental Parameter | Date | Sky Condition | Elevation | Not Watered | Watered |
|---|---|---|---|---|---|
| Air Temperature I (°C) | Aug-17 | Overcast | High | 21.7 [a] ± 0.07 | 21.7 [a] ± 0.07 |
| | | | Intermediate | 21.4 [b] ± 0.07 | 21.4 [b] ± 0.07 |
| Soil Temperature I (°C) | Aug-17 | Overcast | High | 20.6 [a] ± 0.15 | 20.7 [a] ± 0.15 |
| | | | Intermediate | 20.4 [a] ± 0.15 | 20.4 [a] ± 0.15 |
| Air Temperature II (°C) | Aug-20 | Overcast | High | 21.1 [a] ± 0.3 | 20.7 [a] ± 0.3 |
| | | | Intermediate | 20.6 [a] ± 0.3 | 20.9 [a] ± 0.3 |
| Soil Temperature II (°C) | Aug-20 | Overcast | High | 21.1 [a] ± 0.2 | 21.4 [a] ± 0.2 |
| | | | Intermediate | 21.1 [a] ± 0.2 | 21.2 [a] ± 0.2 |
| Air Temperature I (°C) | Jul-20 | Cloudless | High | 22.5 [a] ± 0.2 | 22.5 [a] ± 0.2 |
| | | | Intermediate | 22.3 [a] ± 0.2 | 22.3 [a] ± 0.2 |
| Soil Temperature I (°C) | Jul-20 | Cloudless | High | 19.6 [a] ± 0.4 | 19.5 [a] ± 0.4 |
| | | | Intermediate | 19.1 [a] ± 0.4 | 19.8 [a] ± 0.4 |
| Air Temperature II (°C) | Jul-30 | Cloudless | High | 24.1 [a] ± 0.7 | 22.9 [a] ± 0.7 |
| | | | Intermediate | 22.9 [a] ± 0.7 | 23.4 [a] ± 0.7 |
| Soil Temperature II (°C) | Jul-30 | Cloudless | High | 20.9 [a] ± 0.7 | 19.9 [a] ± 0.7 |
| | | | Intermediate | 20.7 [a] ± 0.7 | 20.1 [a] ± 0.7 |

Table 13. The mean values for several environmental variables across treatments of the substrate experiment implemented at Brown Mill Pond Atlantic white-cedar wetland in Rye, New Hampshire (2001). The mean value for each environmental variable is reported plus or minus the standard error. Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$).

| **Environmental Parameter** | **Tussock Sedge** | **Moss-Litter** |
|---|---|---|
| Soil Moisture after One Week without Rain ($g\ H_2O$/ g dry soil) | $5.09^{a} \pm 0.21$ | $4.40^{b} \pm 0.21$ |
| % Change in Soil Moisture after One Week without Rain | $0.4^{a} \pm 6.8$ | $4.9^{a} \pm 6.8$ |
| pH (July 11, 2001) | $5.14^{a} \pm 0.17$ | $4.58^{b} \pm 0.17$ |
| pH (August 22, 2001) | $4.98^{a} \pm 0.19$ | $4.21^{b} \pm 0.19$ |
| Redox Potential (mV) | $452^{a} \pm 16$ | $464^{a} \pm 16$ |

Table 14. The mean air and soil temperatures across all treatments of the substrate type experiment implemented at Brown Mill Pond Atlantic white-cedar wetland in Rye, New Hampshire (2001). Observation I and II obtained in overcast conditions (August 17 and 20 respectively) and cloudless conditions (July 20 and 30 respectively). The mean value for each temperature is reported plus or minus the standard error. Means with the same letter are not significantly different as a result of analysis of variance ($\alpha = 0.05$).

| **Environmental Parameter** | **Date** | **Sky Condition** | **Tussock Sedge** | **Moss-Litter** |
|---|---|---|---|---|
| Air Temperature I (°C) | Aug-17 | Overcast | $21.6^{a} \pm 0.14$ | $21.5^{a} \pm 0.14$ |
| Soil Temperature I (°C) | Aug-17 | Overcast | $20.7^{a} \pm 0.14$ | $20.3^{a} \pm 0.14$ |
| Air Temperature II (°C) | Aug-20 | Overcast | $20.3^{a} \pm 0.3$ | $20.6^{a} \pm 0.3$ |
| Soil Temperature II (°C) | Aug-20 | Overcast | $21.3^{a} \pm 0.16$ | $21.1^{a} \pm 0.16$ |
| Air Temperature I (°C) | Jul-20 | Cloudless | $22.6^{a} \pm 0.25$ | $22.6^{a} \pm 0.25$ |
| Soil Temperature I (°C) | Jul-20 | Cloudless | $19.8^{a} \pm 0.41$ | $19.5^{a} \pm 0.41$ |
| Air Temperature II (°C) | Jul-30 | Cloudless | $23.7^{a} \pm 0.73$ | $23.5^{a} \pm 0.73$ |
| Soil Temperature II (°C) | Jul-30 | Cloudless | $22.0^{a} \pm 1.0$ | $19.3^{a} \pm 1.0$ |

the percent change in soil moisture for both substrate types was similar ($F_{sub\ type} = 0.2$, df = 1, $p > 0.05$; Table 13).

Neither mean air temperature ($F_{sub\ type} = 0.2\text{-}0.6$, df = 1, $p > 0.05$) nor mean soil temperature ($F_{sub} = 0.4\text{-}3.9$, df =1, $p > 0.05$) differed significantly between the tussock sedge and moss-litter substrates during the first and second observations on overcast days (Table 14). Moreover differences in mean air ($F_{sub\ type} = 0.03\text{-}0.6$, df = 1, $p > 0.05$) and soil ($F_{sub\ type} = 0.4\text{-}4.2$, df = 1, $p > 0.05$) temperature were also not significant on cloudless days for both observations days (Table 14). Moss-litter substrate was more acidic (pH 4.58 and 4.21 respectively) than tussock sedge substrate (pH 5.14 and 4.98 respectively; $F_{sub\ type} = 5.28$, df =1, $p < 0.05$) at the first observation and the second observation ($F_{sub\ type} = 8.38$, df =1, $p < 0.05$; Table 13). Soil redox potential did not significantly differ between substrates ($F_{sub\ type} = 0.3$, df =1, $p > 0.05$; Table 13).

## Discussion

The research presented here is consistent with the hypothesis that Atlantic white-cedar seedling distribution is influenced by a topographic moisture gradient. The work does not confirm, however, that moss-litter hummocks are better substrates for seedling survival and growth than tussock sedge hummocks. The reasons for these assertions are elaborated below.

### Complex Microtopographic Gradient

At Brown Mill Pond, position on hummocks relative to the water table reflected a multi-factor moisture gradient, with both soil moisture and pH decreasing with elevation. This is consistent with other studies that demonstrated complex microtopographic gradients in cedar wetlands (Ehrenfeld 1995a, Mylecraine and Zimmermann 2000).

According to Ehrenfeld (1995b), elevation may be considered the 'master variable' informing the variation in physical and chemical conditions encountered by wetland plant species. Ehrenfeld (1995a) quantified changes in surface substrate conditions with respect to height above the water table in cedar wetlands within the Lebanon State Forest, New Jersey, and found soil moisture decreased while redox potential increased with elevation. While soil pH has not been previously measured in relation to soil moisture in cedar wetlands, Etherington (1982) indicates that moisture and soil pH are inextricably linked. In fact, as acid soils dry out, soil pH typically declines and the peat becomes more acidic (Etherington 1982; pp. 94-95). This is evidenced at Brown Mill Pond where soil pH paralleled moisture patterns on moss-litter hummocks. More specifically, by August the driest treatment, the high elevation-not watered treatment, was characterized by the most acidic soil (3.9) compared to all other treatments (~ 4.6-4.8).

Watering at Brown Mill Pond modified microsite conditions, especially those at high elevations. Watering not only increased soil moisture, but it also changed soil chemistry, in particular increasing soil pH and decreasing redox potential. For instance, by August, continuous watering at high elevations had resulted in a higher soil pH, making the high elevation-watered treatment similar to the soils in the intermediate treatments. Furthermore, plots that had been watered had significantly more reduced (i.e., lower redox potential ~ 446 mV) soil than plots without watering (~ 486 mV). However, these redox values were similar to those of "drier" hummock tops in New Jersey (450-500 mv; Ehrenfeld 1995a). This suggests that none of the watered plots in this experiment, at the end of July, experienced very reduced conditions indicative of flooding but rather slightly reduced conditions as a result of supplemental watering.

**Seedling Response in Elevation-Moisture Experiment**

First Year Seedlings In this study, first year seedlings responded to the complex moisture gradient as well as the watering modification as it affected the high elevation plots. Watering at higher elevations appears to have created comparable conditions to the intermediate elevation treatments and this was reflected in the similar seedling emergence among all treatments except the high elevation-not watered treatment. More specifically, by the end of the summer growing season at Brown Mill Pond, cedar achieved better seedling emergence when seeds were watered at high elevations or were sown at intermediate elevations, 17-22 cm above the water table. These results are consistent with the work of Korstian and Brush (1931) which indicated first year cedar seedlings died on taller hummocks as a result of inadequate moisture during the summer. At Brown Mill Pond, however, small-scale variation in elevation, microtopography, not only affected moisture availability but it also influenced soil pH.

The causal relationship between moisture and pH noted previously presents the question: which factor (i.e., lack of moisture or low pH) influenced the seedlings' response in the high elevation-not watered treatment at Brown Mill Pond? Few studies have looked at pH alone as a factor determining cedar seedling success. However, laboratory experiments found that soil pH, ranging from 3 to 5, did not explain differences in cedar seed germination (Boyle and Kuer 1994). Furthermore, Little (1950) reported that cedar was confined to acidic peat soils, with a pH ranging from 3.5 to 5.5, in the field. In accordance with these studies and Kuser and Zimmermann's (1995) research, I suggest that the results obtained at Brown Mill Pond indicate that soil moisture was the primary limiting factor to natural regeneration of cedar.

While the end-of-season patterns in seedling emergence may ultimately be the most relevant to successful cedar establishment, the seasonal patterns indicate that seedling emergence is dynamic over the growing season and responds to early flooding as well as later drought. In June, many intermediate elevation plots were naturally flooded for approximately two weeks which probably contributed to the relatively low emergence (i.e., percentage of plots with emergence and number of emerged seedlings) at these elevations initially and the slow increase in emergence as the water table declined over the season. The opposite trend was shown in the high elevation-not watered treatment which had high initial emergence but experienced a sharp decline over time in the percentage of plots with emergence and total number of emerged cedar seedlings. Emergence (i.e., number of seedlings tallied) at any point in time was a function of the number emerged *and* number died. It was not possible to quantify mortality in any of the treatments, as seedlings emerged *and* died throughout the growing season; individuals were not marked and tracked in this experiment. Nonetheless, number of emerged seedlings and number of plots with seedlings declined over time only in the high elevation-not watered treatment, and this was assumed to be a result of increased mortality as well as reduced emergence in this treatment. In contrast, the high elevation-watered treatment did not demonstrate this late season decline, indicating that decline in emergence was minimized by supplemental watering.

The results of the seedling emergence experiments must be interpreted with caution because contamination of control plots precluded the determination of baseline seedling emergence. Without baseline (natural) emergence in each treatment, we cannot determine whether numbers of emerging seedlings were determined by the experimental factors alone or by differential dispersal among microsites due to seeds' tendency to move downslope or be removed by a high water table in the spring. It is possible, however, that dispersal was relatively constant among all microsites and that baseline emergence was comparable among all treatments.

Another limitation of the seedling emergence study was its restriction to a single growing season. The short-term nature of this study, along with cedar's reputation for delayed germination (Little 1950, Kuser and Zimmermann 1995) may help explain the overall low seedling emergence rates across both experiments and all treatments. In addition to delayed germination, low seed viability could account for such markedly low emergence across both experiments. It is widely known that cedar seed viability is variable (Laderman 1989, Mylecraine and Zimmermann 2000). Despite these potential restraints to germination and establishment, seedling emergence patterns at Brown Mill Pond supported trends witnessed in the older seedlings (i.e., second year seedlings) in regard to the experimental treatments.

<u>Second Year Seedlings</u> The second year seedling experiments did not suffer the same difficulties as the emergence experiments. This experiment clearly demonstrated that second year seedlings responded to the complex moisture gradient at Brown Mill Pond. More specifically, seedlings grew less in terms of height, branch number, and biomass when not watered and located 35-40 cm above the water table than when they were watered and located at the same "high" elevation or located at the "intermediate" elevation (17-22 cm above the water table). Furthermore, the greatest seedling mortality at Brown Mill Pond occurred in the high elevation-not watered treatment. This finding is consistent with indications that hummock tops, especially litter-covered hummocks such

as those at Brown Mill Pond, are more drought prone and may be associated with cedar mortality, especially during dry years (Ehrenfeld 1995a). Moreover, these results demonstrate a similar trend to that displayed by the first year seedlings, with the high elevation-not watered treatment reducing overall cedar seedling establishment.

Comparison to 2000 Seedling Survey It was assumed that the physical conditions that resulted in the distribution of cedar seedlings in the survey were those that prevailed during the experiment. The lower emergence of first year individuals and slower growth and greater mortality of second year seedlings in the high elevation-not watered treatment are consistent with the field survey (Chapter I) which had suggested that higher elevations (i.e., > 30 cm) relative to the water table were less favorable for seedlings (Chapter I). However, mortality of second year seedlings in the high elevation-not watered treatment was not severe enough to produce the patterns observed in the field survey, which indicated a near absence of seedlings at high elevations. This inconsistency may be explained by the generally more vigorous growth of transplanted individuals versus naturally established individuals (i.e., reference seedlings). Several factors may account for this difference. First, perhaps the root development of transplants was enhanced due to their initial establishment in a greenhouse. Second, it is possible that cutting the hole for the plugs of transplanted seedlings severed roots that potentially would have competed with transplants. Third, two rounds of dilute foliar fertilization applied during the first month of the experiment may have promoted the growth of transplanted seedlings. Lastly, even after fertilization and watering ended, the introduction of commercial peat (to fill in around transplanted root systems) may have influenced transplants' growth.

**Seedling Response to Substrate Types**

First Year Seedlings At the end of the growing season seedling emergence was similar in the moss-litter and tussock sedge substrates. Initially, in June, seedling emergence was greater in the moss-litter substrate than the tussock sedge but over the growing season seedling emergence declined in the moss-litter plots. Either greater mortality of seedlings or lower seedling emergence—or both—could account for the decline over time. Overall, substrate type had little to no effect on cedar seedling emergence by the end of one growing season.

Second Year Seedlings Experimental seedlings grew at least as much and, for some growth measures more, on tussock sedge substrate than on moss-litter substrate. For instance, although final seedling biomass did not differ between substrate types, percent increase in biomass was significantly greater for seedlings grown in tussock sedge than those in moss-litter substrate.

Comparison to 2000 Seedling Survey The weak substrate type effect on seedling emergence and performance of second year individuals was in contrast to expectations based on the 2000 survey (Chapter I) and other cedar studies that indicate cedar prefer peat soils for establishment (Korstian and Brush 1931, Little 1950, Allison and Ehrenfeld 1999). Based on the absence of seedlings on tussock sedge hummocks in the Brown Mill Pond seedling distribution survey, either seedling emergence failure or seedling mortality were expected on tussock sedge hummocks. Seedling success on the two substrate types was not only inconsistent with the 2000 field survey (Chapter I), but it was also inconsistent with the significant differences in soil moisture and pH between the substrates. The success of cedar on both substrates suggests that these physical differences did not influence cedar establishment and growth.

There are several explanations for the inconsistency between the field survey and experiment. First it is possible that the experiment did not include all relevant life history stages. More specifically, it is possible that first year cedar seedlings on tussock sedge hummocks experience mortality their first winter as that stage of growth was undocumented in this study. It is likely, however, that the experimental results were comprehensive, and thus this inconsistency is a sharp reminder of the limitations of observational studies, such as seedling distribution surveys. For example, the results of the discriminant analysis are somewhat misleading (Chapter I). It is possible that other variables could have been correlated with substrate, thereby explaining the absence of seedlings on tussock sedge hummocks. In other words, the absence of cedar seedlings on tussock sedge hummocks may be determined by other factors besides the tussock sedge substrate itself. In fact data presented in Chapter I suggested that the size of tussock sedge hummocks may better explain the absence of the cedar on tussocks than the nature of the substrate. The size hypothesis suggests that the wind-dispersed cedar seed would more likely contact the larger moss-litter hummocks than the smaller tussock sedge ones. The size hypothesis, however, only partially explained the absence of seedlings on tussock sedge hummocks (see Chapter I for details). Thus, there are several additional hypotheses. First, dispersal may be unsuccessful on tussock sedge hummocks because of the dense graminoid vegetation on these hummocks. This hypothesis is weak as wetland species are known to disperse successfully onto tussock sedge hummocks and establish (Lord and Lee 2001). Second, it is possible that differential herbivory among the moss-litter and tussock sedge hummocks explains the lack of seedlings on tussocks. Perhaps, tussocks provide herbivores with more protective cover than moss-litter hummocks resulting in greater grazing of seeds on tussocks. In summary, the underlying factors explaining the lack of seedlings on tussock sedge hummocks naturally remains unclear and further experimentation will be necessary to determine them.

## Implications

Studies such as this contribute to the management and conservation of cedar populations. Placing the bounds on cedar's "safe sites" for germination, emergence, and establishment will facilitate efforts to regenerate or restore cedar populations. According to Kuser and Zimmermann (1995), outplanting cedar seedlings or stecklings (e.g., rooted cuttings) may be used in the foreseeable future in restoration projects. In order for these restoration efforts to be successful the factors influencing cedar's presence and survival must first be determined through rigorous field experiments, such as those implemented in this New Hampshire cedar swamp.

## Conclusion

These field experiments have shown that elevation above the water table influences soil moisture and pH which, in turn, likely influence the establishment success of Atlantic white-cedar. In contrast to an earlier field survey, substrate type was shown to have little effect on cedar's establishment patterns. The experimental results together with those of the field survey have suggested that sufficient moisture and correlated changes in pH as well as hummock area were determining factors in successful cedar recruitment at Brown Mill Pond.

## CHAPTER III

## VARIATION IN THE HYDROLOGICAL REGIME AND ITS ASSOCIATION WITH SPECIES COMPOSITION AND STAND STRUCTURE


### Abstract

Few studies have quantified the hydrological regime of an Atlantic white-cedar wetland. This study measured variation in water table depth and soil moisture in order to characterize the hydrological regime within five cedar communities previously identified at Brown Mill Pond in Rye, New Hampshire: *pond edge*, *cedar I*, *cedar II*, *cedar-red maple*, and *mixed conifer community*. Associations between hydrology and species composition as well as stand structure were investigated. The relationship of the water table of each community with that of the pond was also determined.

In the 1999 and 2000 growing seasons, the five communities were measured monthly for water table depths and soil water content, which was determined gravimetrically. The water table depth measurements were standardized to elevations relative to mean sea level in order to determine the degree to which the water table of each of the communities reflected that of the pond.

This research established an association between hydrology and species composition and stand structure at Brown Mill Pond. The highest water table and wettest peat were located in the pond edge community while the lowest water table and driest peat were located in the mixed conifer community. The remaining communities, cedar I

and II and cedar-red maple, were intermediate in water table depth and soil moisture. Differences in water table levels and soil moisture among cedar communities likely explained variation in species composition and stand structure. The pond edge community was the only community at Brown Mill Pond with continuous establishment of cedar and red maple. I expect that the continuous recruitment of cedar was partially explained by the high water table in this community. I hypothesized that a high water table caused mortality of older stems which produced and maintained a discontinuous canopy that in turn facilitated continuous cedar recruitment. In the drier mixed conifer community, continuous establishment of eastern hemlock and red spruce was evident beneath a closed cedar canopy. The recruitment success of these species is likely a result of the greater depth to water table and drier peat in this community.

Standardization of all water table measurements to elevation above mean sea level showed that, in all communities, the water table had similar elevation through two growing seasons. Water table fluctuations were similar in all communities and in Brown Mill Pond suggesting hydrological linkage throughout the system.

## Introduction

Atlantic white-cedar (*Chamaecyparis thyoides* (L.) BSP.), a rare, freshwater wetland tree species, generally grows in swamps that are defined by a network of slightly elevated hummocks and depressions or hollows (Laderman et al. 1987, Sheffield et al. 1998). Cedars occur on the hummocks and are generally absent from the frequently water-filled hollows (Little 1950, Ehrenfeld 1995b, Kuser and Zimmermann 1995, Allison and Ehrenfeld 1999). These wetlands are characterized by hydric, organic peat that is seasonally flooded by acidic, nutrient-poor water (Korstian and Brush 1931, Laderman 1989). The organic surface soil horizon may be as thick as 3 m, a result of low decomposition rates in the acidic, frequently flooded conditions (Stoltzfus and Good 1998).

Typically, standing water is present in hollows from early spring to mid summer, but is absent by the end of the growing season in most years. Water table depths, however, vary considerably among wetlands and years (Laderman 1989). Golet and Lowry's (1987) seven year study of the hydrology of several cedar wetlands in Rhode Island is the only long-term research published on this subject. Their research indicated that the mean annual water level ranged from 13 cm above to 11 cm below the ground in hollows, and the duration of surface flooding varied from 18% to 76% of the growing season. Changes in water level were strongly determined by variations in annual precipitation, which accounted for 85% to 92% of water level variation. Depth to water table was related to additional factors such as ground water contribution, total transpiration, soil properties, and microtopography.

Soil properties of the organic peat typically found in cedar wetlands influence the hydrological regime in several ways (Damman 1987). The botanical composition (e.g., *Sphagnum*, moss, moss-sedge, or woody peat) along with the degree of humification of the peat affect the soil water content as well as the hydraulic conductivity. Specifically, as peat decays (i.e., fiber content decreases) and becomes more compact (i.e., bulk density increases) water content and hydraulic conductivity declines (Ehrenfeld 1995a). In this way, decay and compaction of peat determines how much water can be stored in peat. In cedar wetlands water is stored in peat and hollows. In late summer, when evapotranspiration exceeds precipitation, lowering the water table below the ground surface, water stored in peat becomes critical to obligate wetland species, such as cedar (Damman 1987).

Hydrology greatly influences species composition within cedar wetland systems (Korstian and Brush 1931, Laderman 1989, Ehrenfeld and Schneider 1990, Ehrenfeld 1995b). Cedar is an obligate wetland species (Phillips et al. 1998) and is adapted to particular water level fluctuations (Kuser and Zimmermann 1995, Mylecraine and Zimmermann 2000). Although previous studies have suggested that hydrological factors, such as water table depth and flood duration, are important to cedar's long-term persistence, few studies thus far have quantified sufficient water table depths or soil moisture. Moreover, few studies have monitored water table activity in cedar wetlands over several growing seasons (Golet and Lowry 1987).

A size and age structure analysis of cedar communities at Brown Mill Pond, in Rye, New Hampshire, indicated that successful cedar regeneration was occurring in one stand, the *pond edge community*, where the canopy was discontinuous (Gengarelly 1999). I hypothesized that hydrology was the mechanism permitting cedar establishment at the pond edge. Specifically the discontinuous canopy may be maintained by occasional mortality of older stems induced by high water levels. This study tests the hypothesis that the water table depth and soil moisture content is higher in the pond edge community than all other communities at Brown Mill Pond.

Brown Mill Pond is an important Nature Conservancy ecological reserve with five cedar communities that differ in age and composition. These five communities surround a pond maintained by a dam. For management purposes it is important to determine to what extent all five communities depend on the water table maintained by the dam. Thus, this study also investigates the degree to which the water table fluctuations among communities are similar and whether all communities are hydrologically linked to Brown Mill Pond.

## Methods

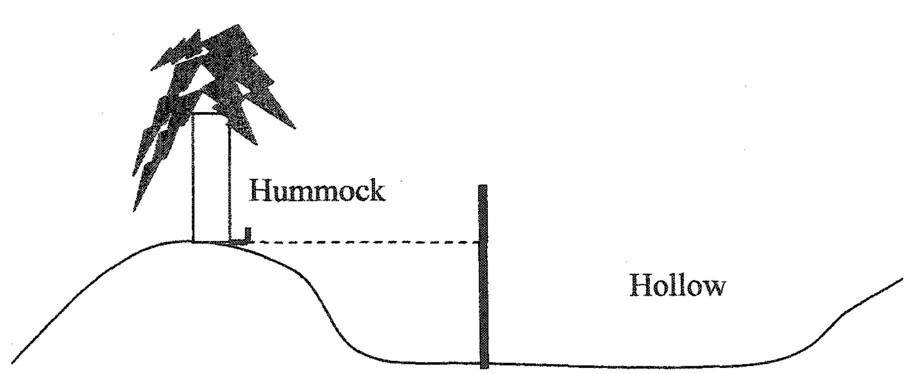
### Study Site: Brown Mill Pond

Brown Mill Pond and associated wetlands are located in Rye (Rockingham County), New Hampshire at an elevation of 30' (9 m) (Sperduto and Ritter 1994). This site is owned by The Nature Conservancy. Soil is a Chocorua mucky peat and hummock-hollow microtopography is well-developed (Kelsea and Gove 1994). Cedar occupies ca. 50 acres (20 ha) of this 110 acre (45 ha) wetland. Cedar forms a continuous canopy in some areas while in others mixes with *A. rubrum* (red maple), *T. canadensis* (eastern hemlock), and *P. rubens* (red spruce). An earlier study (Gengarelly 1999) identified five contiguous communities based on species composition and cedar size: *mixed conifer*, *cedar-red maple*, *cedar I*, *cedar II*, and *pond edge* (Figure 1). The mixed conifer and cedar-red maple stands bordered the upland forest to the south and southwest while cedar I abutted a red maple swamp to the northwest. Cedar II community was centrally situated and encircled by several communities. Unlike the other stands, the pond edge community bordered Bailey Brook and Brown Mill Pond.

### Hydrological Variables

The five communities were analyzed for their water table depths and soil moisture content. Five plots (10 x 10 m) were established randomly within each community (25 total). In each plot, three hummocks and three hollows were sampled for soil water content, which was determined gravimetrically (Slatyer 1970). Surface peat was taken from the highest point of the hummock and the lowest point of the adjacent hollow. Soil was collected in tared aluminum soil tins, which were then sealed with tape, labeled, and transported to lab. Samples were weighed wet the same day and then dried at 105°C for 3 days and weighed again. Water content was calculated based on the mass of these soil samples and expressed as mass of water per unit mass of dry soil.

The elevation of five randomly selected hummocks in each plot was measured in relation to the free water table and hollow soil surface. In order to account for water table fluctuations, measurements were obtained once a month for two consecutive growing seasons (~April-September 1999-2000). When standing water was absent, a small hole (40-50 cm in diameter) was dug with a shovel in order to locate the water table. As water seeps slowly into such holes, pits were left for 24 hours in order to allow the water table to equilibrate. Measurements in 1999 were limited to April-July due to a severe late summer drought that precluded digging holes deep enough to reach the water table. In order to measure hummock-hollow distance, a meter stick was set upon the hollow surface and held upright. A string, set to horizontal using a line level, was drawn from a fixed point on the top of the hummock (galvanized nail tapped into a cedar root) to the meter stick. The water table height above or below the hollow was measured with the meter stick alone (see below).



## Water Table Depths Relative to Mean Sea Level

In order to standardize the water table depth measurements across community types, reciprocal leveling was used to determine the elevation of each nail within each sampling plot relative to mean sea level (i.e., as described by Kavanagh 2001). A tilting level and a fiberglass leveling rod graduated to meters were used. The rod was plumbed with a rod level. A concrete culvert headwall on Love Lane was used as the temporary benchmark. The elevation of the benchmark, 9.927 m above mean sea level, was determined by James Verra, a local surveyor.

These measurements were used to determine the water table elevation relative to mean sea level for all stand types [e.g., (elevation of nail relative to mean sea level) – (distance to the water table) = (elevation of water table relative to mean sea level)]. As the Brown Mill Pond water was contiguous with the water level in the pond edge community, the water table measurements in this stand were used as the indicator of the pond's elevation and helped answer the question: did all five communities depend on the water table that is maintained by the dam?

## Statistical Analyses

A split-plot analysis of variance (ANOVA) was used to compare soil moisture differences and water table fluctuations across communities (main plot) and months (sub-plot) for each year. An interaction between month and community was included as a factor in this repeated measures ANOVA model. The statistical significance of community was determined using the nested term, plot (community), as the error term. Each statistically significant factor was followed by a Tukey multiple comparison test.

A series of one-way ANOVAs were used to compare mean water table differences (adjusted to mean sea level) among communities during each month of measurement in 1999 and 2000. When a significant difference among communities was found a Tukey multiple comparison test followed. Analyses were made using SYSTAT 5.2 for PC (Wilkinson et al. 1992).

## Results

### Soil Moisture Content

Overall, hollow soils were consistently more wet (6.4-8.9 g $H_2O$/ g dry soil) than the hummock soils (2.5-3.7 g $H_2O$/ g dry soil) regardless of community type, month, or year (figures 2-9).

1999 In 1999 hollow soil moisture differed among communities ($F = 6.99$, $df = 4$, $p < 0.01$; Figure 21, Table 15) and across months ($F = 10.50$, $df = 3$, $p < 0.01$; Figure 22, Table 15). Similarly hummock soil moisture demonstrated significant differences among communities ($F = 4.47$, $df = 4$, $p < 0.01$; Figure 23, Table 16) and across months ($F = 12.54$, $df = 3$, $p < 0.01$; Figure 24, Table 16) in 1999.

2000 During the 2000 growing season hollow soil moisture differed among communities ($F = 12.43$, $df = 4$, $p < 0.01$; Figure 25, Table 17) and across months ($F = 3.76$, $df = 4$, $p = 0.05$; Figure 26, Table 17). Hummock soil moisture did not differ among communities ($F = 2.19$, $df = 4$, $p = 0.11$; Figure 27, Table 18) but did differ across months ($F = 14.01$, $df = 4$, $p < 0.01$; Figure 28, Table 18).

Seasonal: month to month variation Variation in hollow soil moisture content across months was different for each year and roughly followed the water table trends. In the drought year of 1999, hollow soil moisture initially was high (~ 8.40 g $H_2O$/ g dry soil, Figure 22) and then abruptly declined in July (6.37 g $H_2O$/ g dry soil, Figure 22).

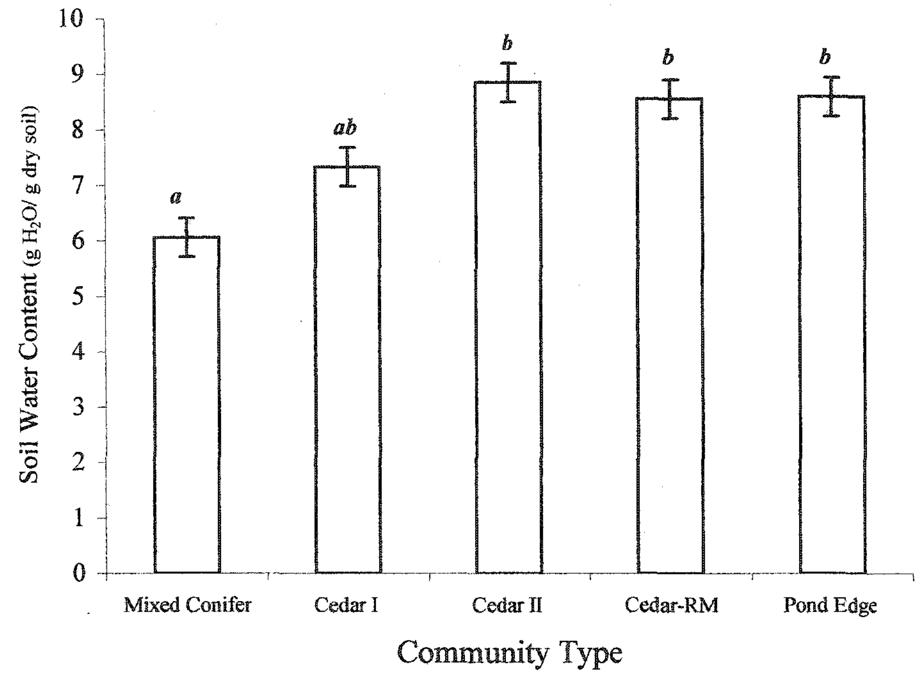



Figure 21. Hollow soil water content for each community type at Brown Mill Pond, Rye, NH, over the 1999 growing season (n= 20; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

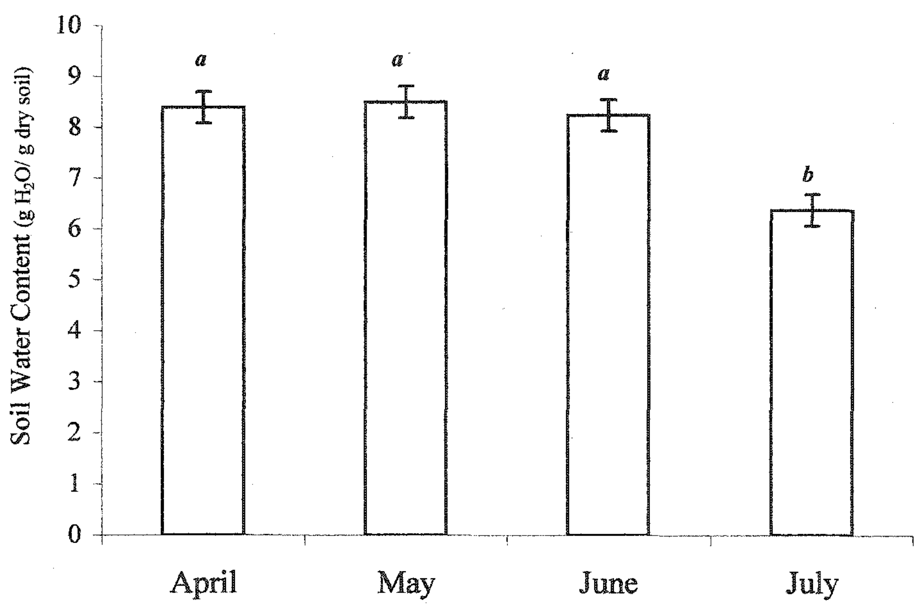



Figure 22. Hollow soil water content for all communities at Brown Mill Pond, Rye, NH, for each month of the 1999 growing season (n=25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

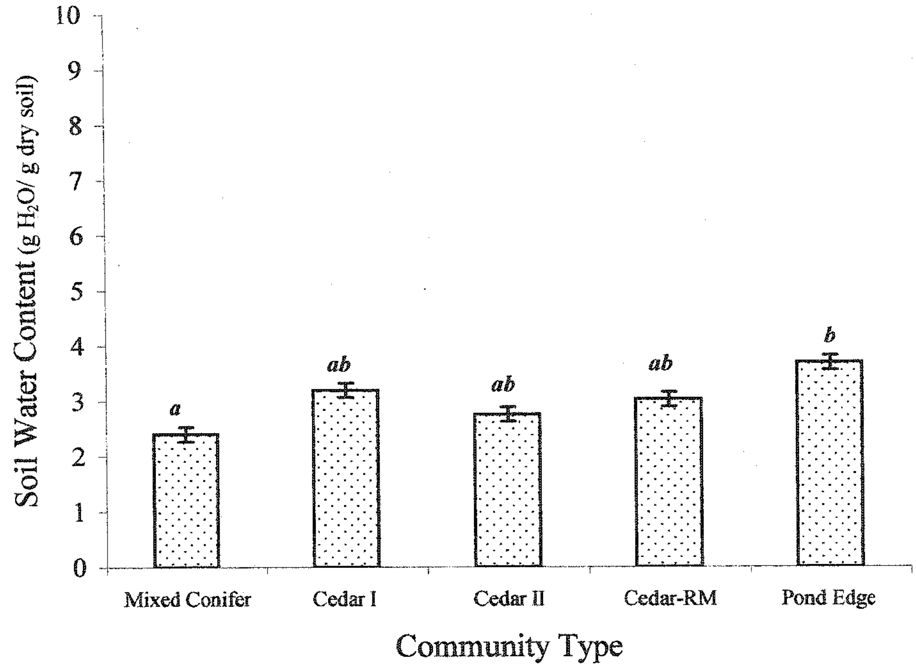



Figure 23. Hummock soil water content for each community type at Brown Mill Pond, Rye, NH, over the 1999 growing season (n= 20; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

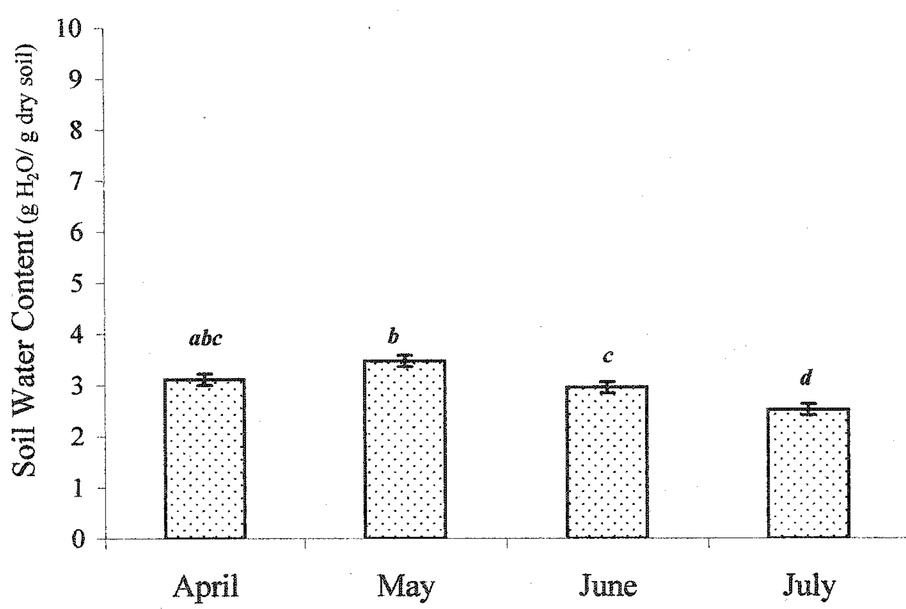



Figure 24. Hummock soil water content for all communities at Brown Mill Pond, Rye, NH, for each month of the 1999 growing season (n=25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

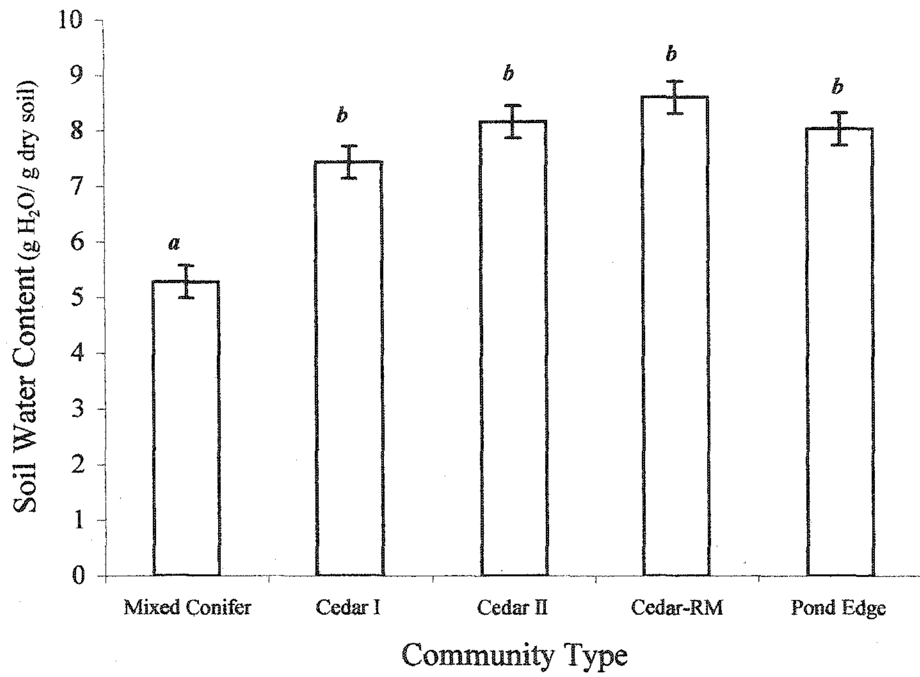



Figure 25. Hollow soil water content for each community type at Brown Mill Pond, Rye, NH, over the 2000 growing season (n= 25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

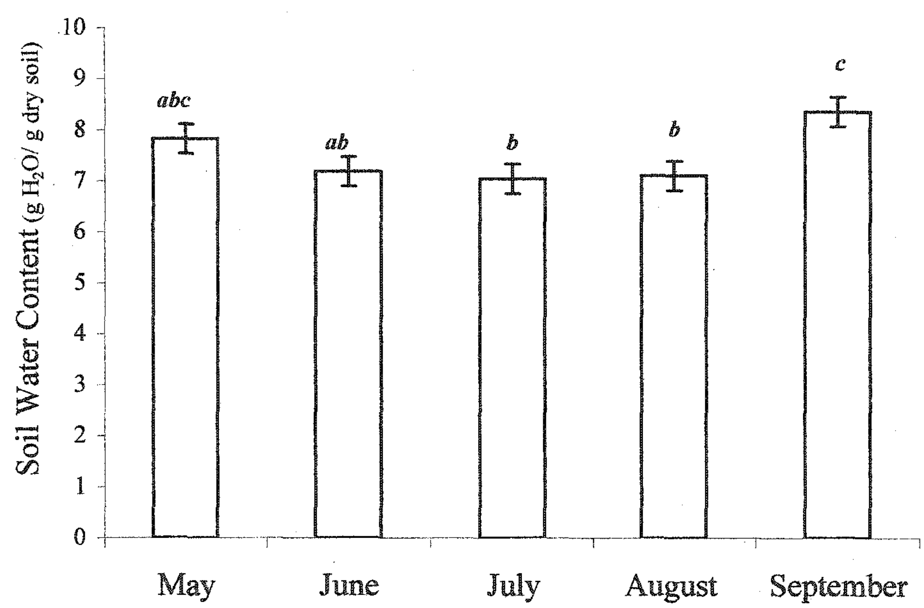



Figure 26. Hollow soil water content for all communities at Brown Mill Pond, Rye, NH, for each month of the 2000 growing season (n=25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

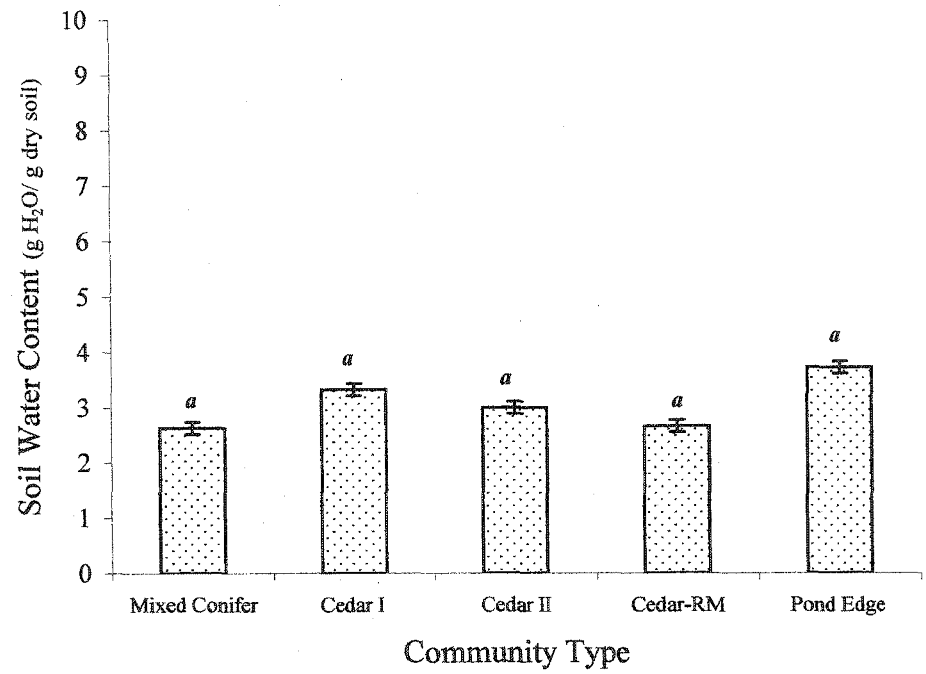



Figure 27. Hummock soil water content for each community type at Brown Mill Pond, Rye, NH, over the 2000 growing season (n= 25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

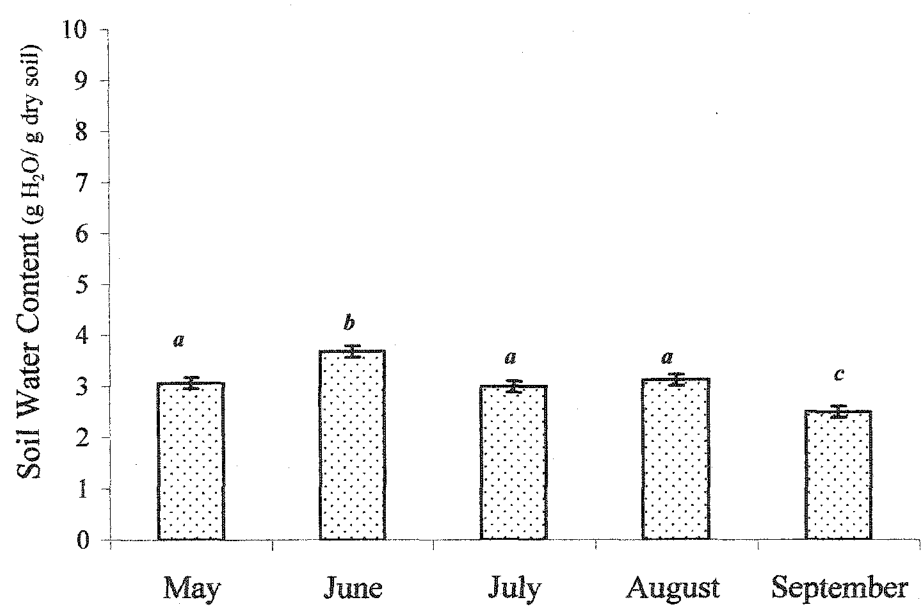



Figure 28. Hummock soil water content for all communities at Brown Mill Pond, Rye, NH, for each month of the 2000 growing season (n=25; error bars = standard error; means with the same letter are not significantly different, $\alpha = 0.05$).

**Table 15.** Results of repeated-measures analysis of variance testing hollow soil moisture differences across stand type and months at Brown Mill Pond, Rye, New Hampshire in 1999.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 110.46 | 27.61 | 6.99 | 0.00 |
| Plot (Stand Type) | 20 | 78.98 | 3.95 | | |
| Subplots | | | | | |
| Month | 3 | 76.48 | 25.49 | 10.50 | 0.00 |
| Month x Stand Type | 12 | 18.50 | 1.54 | 0.64 | 0.80 |
| Error | 60 | 145.63 | 2.43 | | |

**Table 16.** Results of repeated-measures analysis of variance testing hummock soil moisture differences across stand type and months at Brown Mill Pond, Rye, New Hampshire in 1999.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 18.42 | 4.60 | 4.47 | 0.01 |
| Plot (Stand Type) | 20 | 20.62 | 1.03 | | |
| Subplots | | | | | |
| Month | 3 | 11.99 | 4.00 | 12.54 | 0.00 |
| Month x Stand Type | 12 | 3.97 | 0.33 | 1.04 | 0.43 |
| Error | 60 | 19.12 | 0.32 | | |

**Table 17**. Results of repeated-measures analysis of variance testing hollow soil moisture differences across stand type and months at Brown Mill Pond, Rye, New Hampshire in 2000.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 171.24 | 42.81 | 12.43 | 0.00 |
| Plot (Stand Type) | 20 | 68.88 | 3.44 | | |
| Subplots | | | | | |
| Month | 4 | 32.17 | 8.04 | 3.76 | 0.01 |
| Month x Stand Type | 16 | 41.49 | 2.59 | 1.21 | 0.28 |
| Error | 80 | 170.89 | 2.14 | | |

**Table 18**. Results of repeated-measures analysis of variance testing hummock soil moisture differences across stand type and months at Brown Mill Pond, Rye, New Hampshire in 2000.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 21.38 | 5.35 | 2.19 | 0.11 |
| Plot (Stand Type) | 20 | 48.85 | 2.44 | | |
| Subplots | | | | | |
| Month | 4 | 17.76 | 4.44 | 14.01 | 0.00 |
| Month x Stand Type | 16 | 5.84 | 0.36 | 1.15 | 0.32 |
| Error | 80 | 25.34 | 0.32 | | |

Standing water was absent from hollows July- September of 1999 (personal observation). In contrast, during the wet 2000 season, hollow soil was moist initially (~ 7.5 g $H_2O$/ g dry soil May-June, Figure 26) and remained so throughout the season (~7.5 g $H_2O$/ g dry soil July-September, Figure 26).

During the drought year of 1999 and the wet 2000 season, the hummock soil moisture declined over each of these growing seasons (Figures 5 and 9). In both years hummock soil moisture was greatest (~ 3.5 g $H_2O$/ g dry soil; Figures 5 and 9) in the spring (April-June) and then decreased significantly in the summer (July-September) which differed for each year. In July 1999, the driest hummock moisture content (2.51 g $H_2O$/ g dry soil; Figure 24) was documented when moisture measurements ceased due to severe drought. In the wet year of 2000, the driest hummock reading was obtained in September (2.49 g $H_2O$/ g dry soil; Figure 28).

Community Variation Regardless of the year, hollow soil water content was generally lowest in the mixed conifer community (~ 5.7 g $H_2O$/ g dry soil) and similar among the remaining four communities (~ 7.3-8.8 g $H_2O$/ g dry soil, Figures 2 and 6). On the other hand, hummock soil moisture significantly differed between the pond edge community and mixed conifer community in 1999 while no significant differences were found among communities in 2000 (Figure 27). In 1999 the pond edge community had hummocks with the greatest soil moisture (3.7 g $H_2O$/ g dry soil; Figure 23) while the mixed conifer community had hummocks with the lowest soil moisture (2.4 g $H_2O$/ g dry soil; Figure 23). The remaining communities had hummocks with intermediate soil moisture (~ 3.0 7 g $H_2O$/ g dry soil; Figure 23) that did not significantly differ from either the pond edge or mixed conifer communities (Figure 23).

## Water Table

The water table to the hollow surface distance differed in a complex way through space and time (Figures 10, 11, and 12). In 1999 water table-to-hollow distance differed among communities depending on the month in which measurements were taken ($F = 7.35$, $df = 12$, $p < 0.001$ for community*month interaction term; Figure 29, Table 19). During the unusually wet 2000 season, water table-to-hollow distance differed among communities ($F = 2.96$, $df = 4$, $p < 0.05$; Figure 30, Table 20) and months ($F = 178.6$, $df = 4$, $p < 0.001$; Figure 31, Table 20) with no significant interaction ($F = 0.79$, $df = 16$, $p > 0.05$; Table 20).

In general, the lowest water table was found in the mixed conifer community. There, water level was significantly lower than other communities during June and July of the 1999 drought season (13-28 cm below hollow; Figure 29) and during the unusually wet 2000 season (10 cm above hollow; Figure 30). The highest water table was located at the pond edge, with water level significantly higher than the mixed conifer community during the wet 2000 season (21 cm above hollow) (Figure 30). During both seasons, the pond edge water level was not significantly different from that of the adjoining cedar red-maple, cedar I and cedar II communities (Figure 29). The cedar I, cedar II, and cedar-red maple communities typically had intermediate water levels that were similar within each year (Figures 10 and 11).

## Water Table Relative to Mean Sea Level

In 1999 the water table relative to mean sea level was not significantly different among communities at Brown Mill Pond, April through June. In July, however, the water table in the mixed conifer community was significantly lower than all other

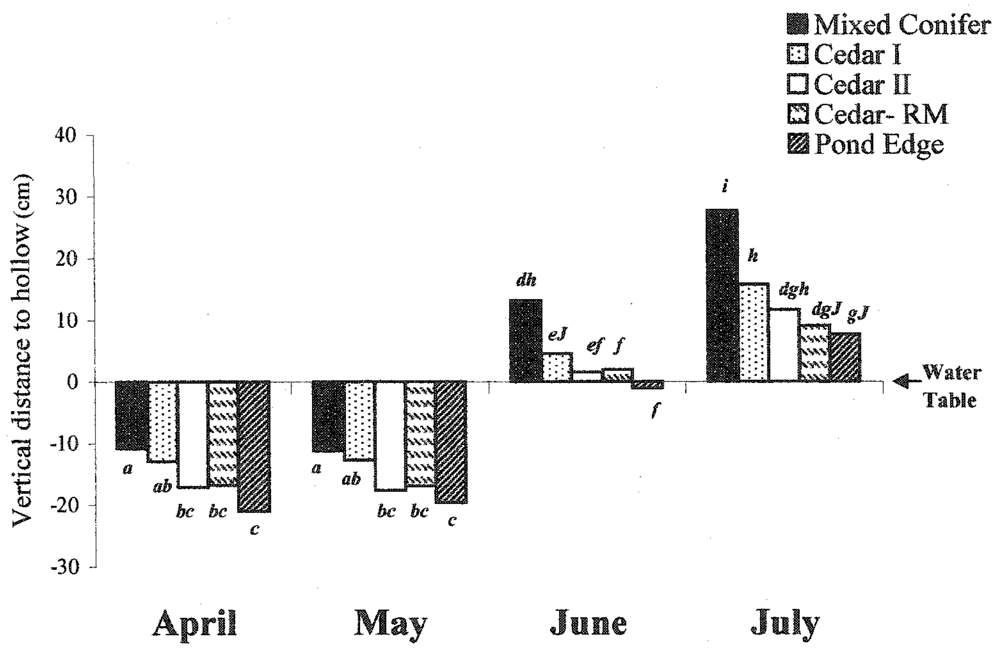



Figure 29. Water table to hollow distance for each community and month of the 1999 growing season at Brown Mill Pond, Rye, New Hampshire. Negative values indicate standing water (hollow is below water table). Means with the same letter are not significantly different, $\alpha = 0.05$ (n = 5).

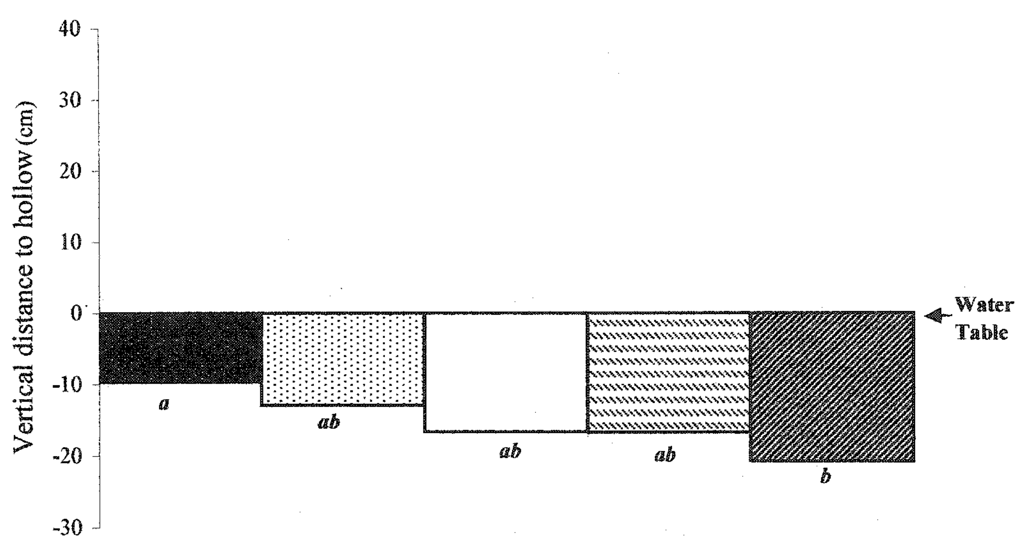



Figure 30. Water table to hollow distance for each community over the 2000 growing season at Brown Mill Pond, Rye, New Hampshire. Negative values indicate standing water (hollow is below water table). Means with the same letter are not significantly different, $\alpha = 0.05$ (n = 25).

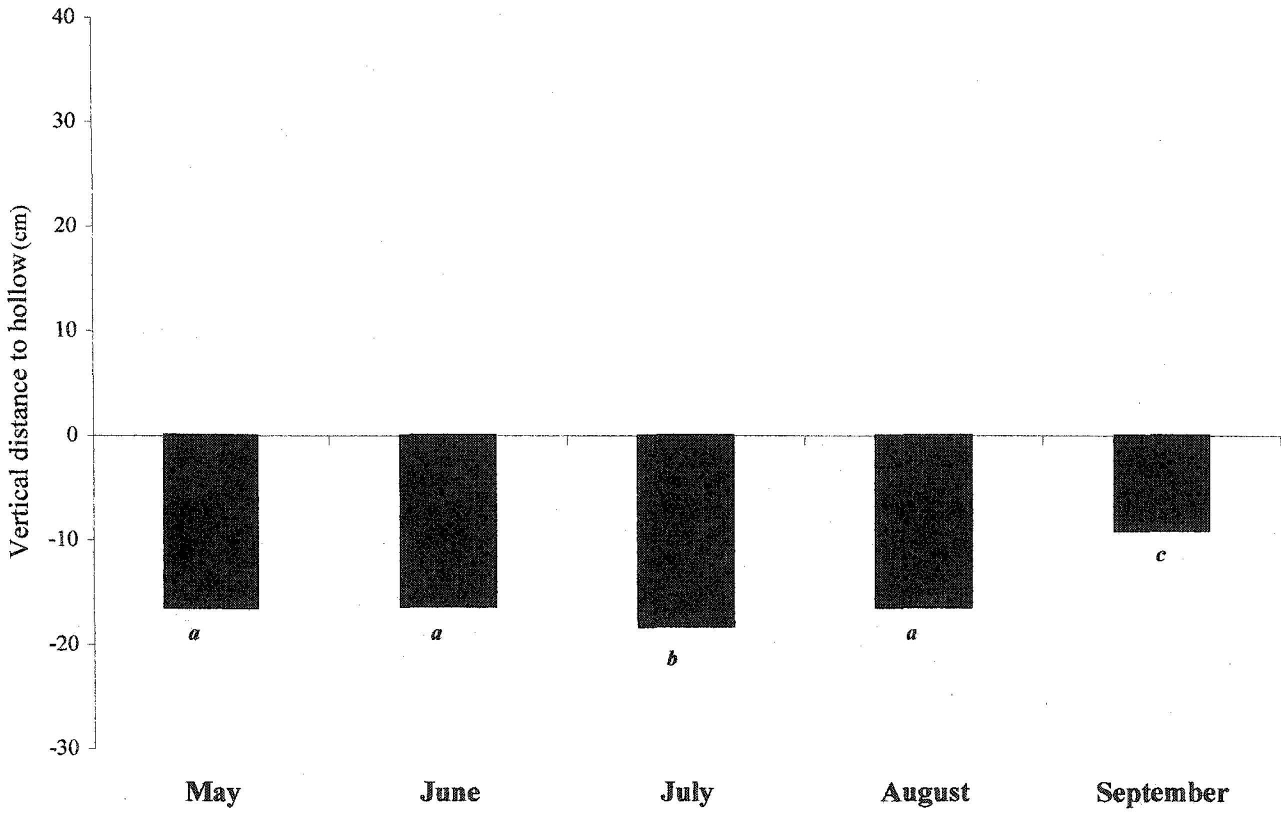



Figure 31. Water table to hollow distance for all communities combined for each month over the 2000 growing season at Brown Mill Pond, Rye, New Hampshire. Negative values indicate standing water (hollow is below water table). Means with the same letter are not significantly different, $\alpha = 0.05$ ($n = 25$).

**Table 19**. Results of repeated-measures analysis of variance testing water table to hollow distance differences across stand type and months at Brown Mill Pond, Rye, New Hampshire in 1999.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 2100.52 | 525.13 | 4.06 | 0.01 |
| Plot (Stand Type) | 20 | 2588.13 | 129.41 | | |
| Subplots | | | | | |
| Month | 3 | 16843.54 | 5614.51 | 1371.70 | 0.00 |
| Month x Stand Type | 12 | 360.93 | 30.08 | 7.35 | 0.00 |
| Error | 60 | 245.59 | 4.09 | | |

**Table 20**. Results of repeated-measures analysis of variance testing water table to hollow distance differences across stand type and months at Brown Mill Pond, Rye, New Hampshire 2000.

| *Source of Variation* | df | SS | MS | F-ratio | p |
|---|---|---|---|---|---|
| Main Plot | | | | | |
| Stand Type | 4 | 1739.36 | 434.84 | 2.96 | 0.04 |
| Plot (Stand Type) | 20 | 2933.66 | 146.68 | | |
| Subplots | | | | | |
| Month | 4 | 1282.48 | 320.62 | 178.63 | 0.00 |
| Month x Stand Type | 16 | 22.64 | 1.42 | 0.79 | 0.69 |
| Error | 80 | 143.59 | 1.79 | | |

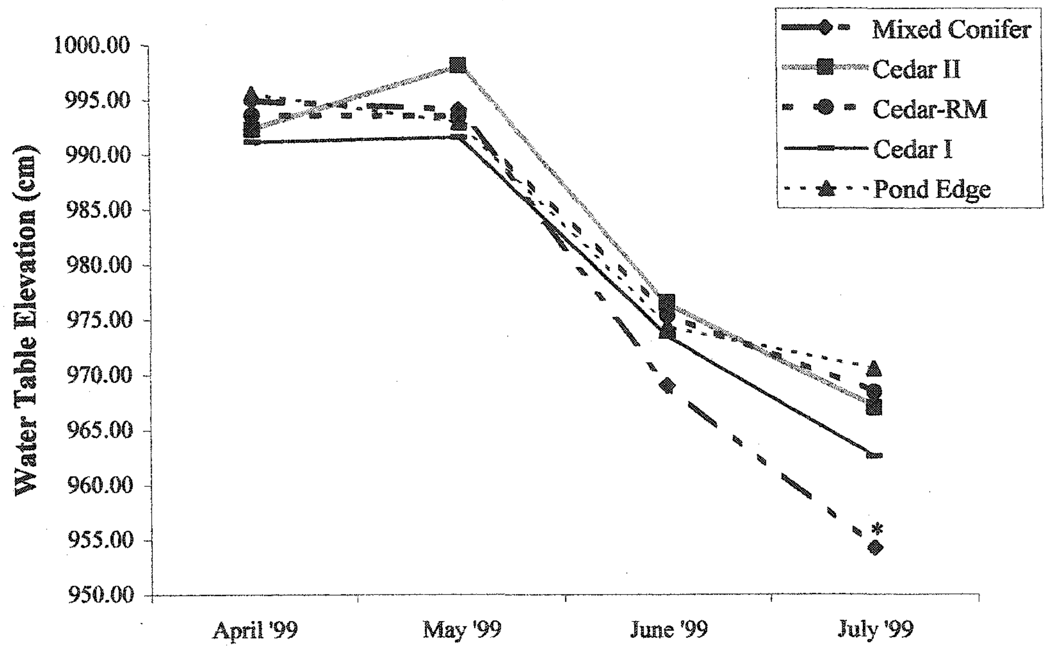



Figure 32. Mean water table elevation relative to mean sea level in all communities at Brown Mill Pond, Rye, New Hampshire during the 1999 growing season. No significant differences were found among communities across months, except in July the mixed conifer water level was considered significantly lower (*)

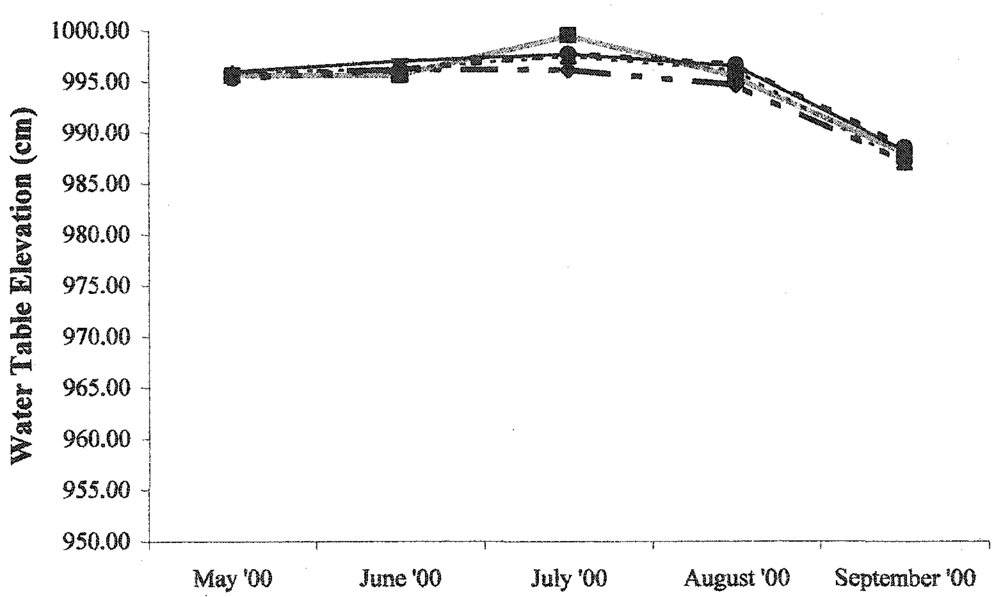



Figure 33. Mean water table elevation relative to mean sea level in all communities at Brown Mill Pond, Rye, New Hampshire during the 2000 growing season. No significant differences among communities were found.

communities (Figure 32). In 2000 the water table was not significantly different among communities throughout the growing season (Figure 33).

## Discussion

### Hydrology

Despite some variability among communities and across years, the highest water table and wettest peat were located in the pond edge community, while the lowest water table and driest peat were located in the mixed conifer community. The remaining communities, cedar I and II and cedar-red maple, were intermediate in water table depth and soil moisture. Differences in water table levels and soil moisture among cedar communities likely explained variation in species composition and stand structure.

Highest Water Table The pond edge community was the only community at Brown Mill Pond with continuous establishment of cedar and red maple (Gengarelly 1999). I expect that the continuous recruitment of cedar is partially explained by the high water table in this community. Two hypotheses concerned with hydrology may offer the best explanations for cedar establishment here. First, it is possible that the current water level has remained high for decades. A routinely high water table is likely to cause continuous stress on the trees and decrease life spans. Thus, hydrology may produce an equilibrium situation in which continuous high water increases tree mortality and concomitantly opens the site for recruitment. Second, it is possible that altered hydrology promoted recruitment. Town of Rye pumping wells within the Bailey Brook watershed may have contributed to long-term declines in water levels (Danna Truslow, personal communication 2003). It is possible that low water levels for several consecutive growing seasons exposed elevated hummocks which became open seed beds and facilitated cohort establishment. This pattern of establishment was observed earlier by Buell and Cain (1943). Regardless of the mechanism that produced the discontinuous canopy in the pond edge community—a stable or lowered water table—continuous cedar recruitment will likely continue unless the canopy closes.

Intermediate Water Table The three communities in which the water table levels were intermediate, cedar I and II and cedar-red maple, were characterized by a cedar canopy. The understory in these communities consisted of red maple and tall shrubs in varying abundance with small amounts of cedar (Gengarelly 1999). These sites were apparently not wet enough to produce a discontinuous canopy with continuous cedar establishment.

Lowest Water Table The mixed conifer community was the only community in which eastern hemlock and red spruce established, apparently continuously, beneath the closed cedar canopy (Gengarelly 1999). The success of these non-wetland species may be due to the greater depth to water table in this community. Hemlock and spruce are not as flood tolerant as cedar and red maple (Burns and Honkala 1990). Furthermore, the lack of cedar regeneration in the mixed conifer community is in agreement with Little (1950) who observed that small, young cedars were not well represented in the understory of a closed canopy.

**Relationship among Water Tables of each Community and the Pond**

The water table relative to mean sea level fluctuated among each community over the 1999 and 2000 growing seasons, with the drought year of 1999 demonstrating an overall decline in all communities. More specifically, in 1999 standing water was absent in all communities by the end of this drought season, whereas in 2000 standing water was found in all communities throughout the growing season (Figures 10 and 11). This is in agreement with a Rhode Island study conducted over seven years that quantified changes of the water table with respect to the land surface and emphasized that water levels varied significantly between years, primarily in response to changes in annual precipitation (Golet and Lowry 1987).

Before cedar management decisions are made, the specific hydrology of a wetland must be considered (Ehrenfeld and Schneider 1990, Mylecraine and Zimmermann 2000). Determining the water table and its fluctuation is critical. The standardized water level measurements at Brown Mill Pond clearly showed that water table elevation and fluctuations were similar among all communities. The only exception was in the mixed conifer community during the 1999 drought when its water table was significantly lower than that of all other stands. Nonetheless, these results indicate that the water table in all communities is strongly associated with the water level of the pond. As Brown Mill Pond is maintained by a dam, from a management perspective it is critical to maintain the dam and water levels in order to ensure the current moisture regime within this wetland.

**Conclusion**

Differences in water table levels and soil moisture among cedar communities likely explain variation in species composition and stand structure, at Brown Mill Pond, an Atlantic white-cedar wetland in Rye, New Hampshire. Furthermore, as Brown Mill Pond is the only cedar wetland in the region with substantial natural regeneration, its conservation is an important management concern (Gengarelly 1999). This research indicated that the overall water regime of all cedar communities at Brown Mill Pond was maintained by the pond water level. Therefore, monitoring water levels and preserving the man-made dam that ultimately controls the pond water level are critical management goals in order to ensure the sustainability of this unique cedar ecosystem.

## SYNOPSIS

Unlike the majority of Atlantic white-cedar wetlands in the northeast USA, the five cedar communities at Brown Mill Pond, New Hampshire, showed variation in structure and regeneration. The substantial natural regeneration in one community offered a rare opportunity to study the biological and physical conditions associated with cedar seedling recruitment in a New Hampshire cedar swamp. My current dissertation research addressed two major objectives: 1. to what extent do the five cedar communities at Brown Mill Pond differ in hydrology and 2 . what are the particular microsite factors influencing cedar recruitment in the pond edge community.

This research established an association between hydrology and species composition and stand structure at Brown Mill Pond (Chapter III). The highest water table and wettest peat were located in the *pond edge community*, while the lowest water table and driest peat were located in the *mixed conifer community*. The remaining communities—*cedar I*, *cedar II*, and *cedar-red maple*—were intermediate in water table depth and soil moisture. These findings supported the hypothesis that water table depth and soil moisture content were higher in the pond edge community than all other communities at Brown Mill Pond. Differences in water table levels and soil moisture among cedar communities likely explain variation in species composition and stand structure. The pond edge community was the only community at Brown Mill Pond with continuous establishment of cedar and red maple. I expect that the continuous recruitment of cedar was partially explained by the high water table in this community. A routinely high water table may cause continuous stress on the trees and decrease life spans. Thus, hydrology may produce an equilibrium situation in which continuous high water increases tree mortality and concomitantly opens the site for recruitment.

A combination of a field survey and field experiments demonstrated that elevation above the water table influences soil moisture and pH which, in turn, likely influence the establishment success of Atlantic white-cedar on hummocks at Brown Mill Pond (Chapters I and II). Both soil moisture and pH decreased with elevation relative to the water table. Cedar seedlings were most common at "intermediate" elevations (10-25 cm above the water table) on hummocks and were less common at higher elevations on these hummocks, which reached heights of up to 60 cm above the water table (Chapter I). Field experiments were consistent with the hypothesis that "high" elevations (> 30 cm above the water table) were less favorable for seedling emergence, establishment, growth, and survival (Chapter II). Watering was found to modify microsite conditions, increasing soil moisture and pH, and to improve seedling performance at high elevations. Thus, lack of sufficient moisture was identified as one of the critical limiting factors in Atlantic white-cedar recruitment.

The field survey indicated a substrate effect on cedar seedling distribution with seedlings absent from *tussock sedge hummocks* and present on *moss-litter hummocks* (Chapter I). In contrast to this observation, the field experiment showed hummock substrate type (i.e., tussock sedge versus moss-litter) to have little if any effect on cedar's establishment patterns. In fact, seedling emergence, establishment, growth, and survival were similar between the two substrate types (Chapter II). The inconsistency between the field survey and experiment indicated a limitation of correlative studies and demonstrated the critical value of rigorous field experiments in conjunction with field surveys.

The lack of correspondence of the field survey and substrate experiment suggested that the absence of seedlings on tussock sedge hummocks is determined by other factors besides the tussock sedge substrate itself (Chapters I and II). Further analysis of survey data suggested that the size of tussock sedge hummocks may better explain the absence of the cedar on tussocks. Tussock hummocks were on average 32% as large as moss-litter hummocks. Thus, the wind-dispersed cedar seed would more likely contact the larger moss-litter hummocks than the smaller tussock sedge hummocks, resulting in a lower frequency of occurrence on the latter (Chapter I).

These experimental results, together with those of the field survey, identify moisture and associated factors plus hummock area as critical factors to successful cedar recruitment at Brown Mill Pond, and show that hummock substrate was not important. Studies such as this contribute to the management and conservation of cedar populations. Placing the bounds on cedar's "safe sites" for germination, emergence, and establishment will facilitate efforts to regenerate or restore cedar populations, a critical management goal as cedar populations are in decline throughout their range.

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